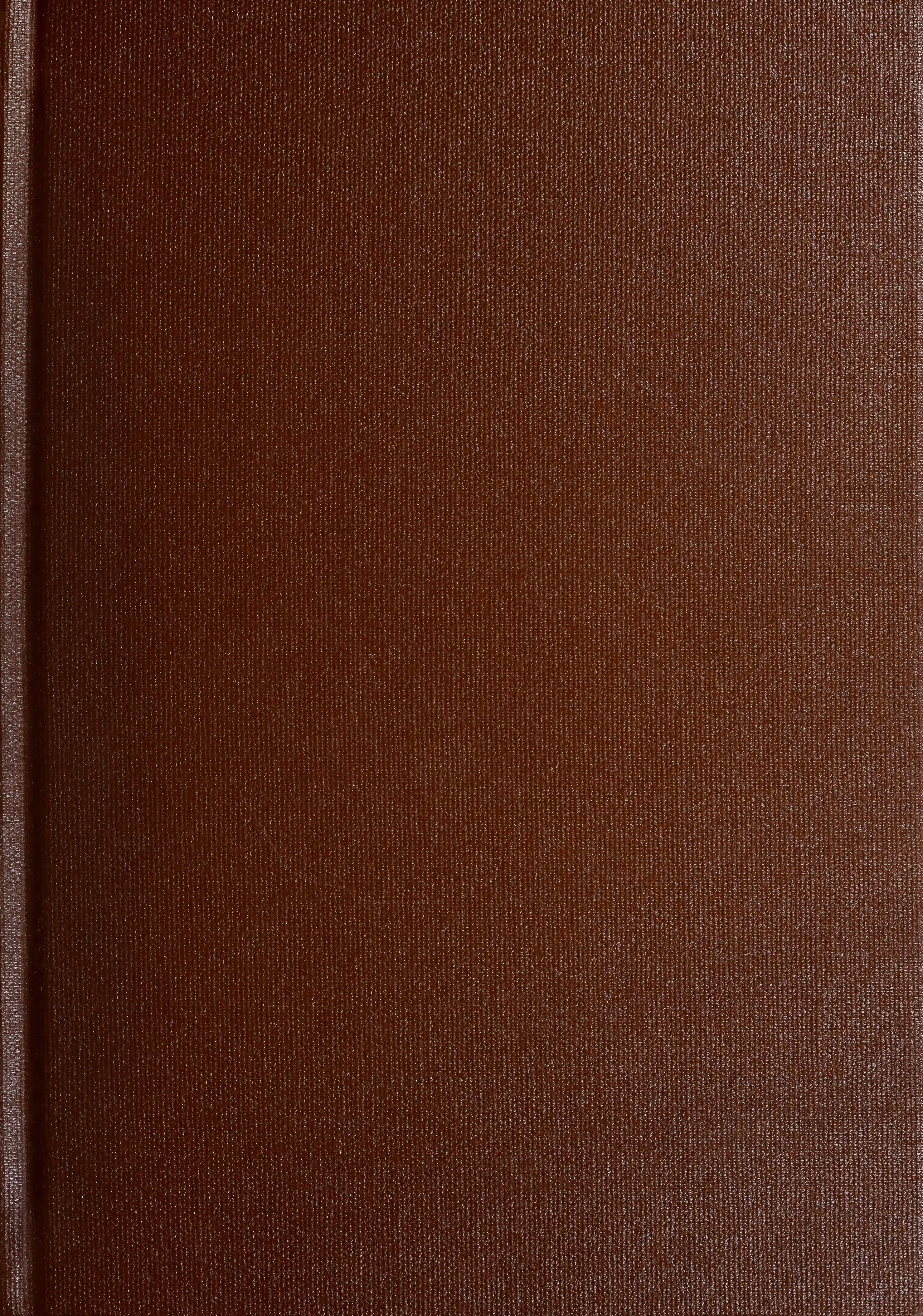




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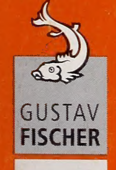
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Phylogeny of southern South American mouse opossums (*Thylamys*, Didelphidae) based on allozyme and chromosomal data

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Abstract

We evaluated the phylogeny of mouse opossums of the proposed genus *Thylamys* using 26 enzymatic loci and standard karyotypes in four of the five recognized species. Allozyme data were analyzed through parsimony, distance, and likelihood methods. Chromosome data showed a conservative diploid and fundamental number in all analyzed taxa (2 n = 14, FN = 20), although the FN differed with respect to other forms of small opossums by having a FN = 24. Parsimony, distance, and likelihood trees confirmed *Thylamys* as a monophyletic group when compared to other Neotropical mouse opossums. The recognition of *T. elegans* at the eastern and western side of the Andean Cordillera is not supported through allozyme analyses, validating Tate's (1933) contention that two species are present. Other reconstructions found *T. pallidior* to be phylogenetically related to *T. elegans* from the western Andes of Chile, while *T. elegans* from Bolivia appeared as the most basal thylamyine. Our data suggest that the latter should again be recognized as a full species, *T. venusta*.

Key words: Phylogeny, *Thylamys*, South America, allozymes, chromosomes

Introduction

Marsupials of the genus *Marmosa* Gray, 1821 have been under taxonomic revision since Tate (1933) recognized five species groups: *murina*, *cinerea*, *noctivaga*, *microtarsus*, and *elegans*. Tate (1933) based these groupings on morphological characters and suggested that they appeared to represent monophyletic lineages with the exception of *microtarsus*, which might be part of the *elegans* group. Based on morphological, serological, and chromosomal studies some authors have suggested that these species groups approximate the genera *Marmosa* (sensu stricto; Tate's *murina* group), *Micoureus* (Lesson, 1842, Tate's *cinerea* group), *Thylamys* (Gray, 1843, Tate's *elegans* group), *Marmosops* (Matschie, 1916, Tate's *noctivaga* group), and *Gracilinanus* (Gardner and Creighton, 1989, Tate's *microtarsus* group; Creighton 1984; Reig et al. 1987; Gardner and Creighton 1989). Morphologically, *Thylamys* spp. differentiate from the rest of mouse opossums by their three-colored pattern, their capacity to store fat in the tail (at least in temperate forms), the small size of the feet and claws in relation to the body, and the slender nasals that do not expand at the maxillo-frontal suture (Fig. 1; Creighton 1984; Tate 1933). The skull of *Thylamys* has a large tympanic bulla and a narrowed interorbital region in comparison to other marmosines (Tate 1933).

Marmosine opossums comprise a species-rich assemblage consisting of 33 currently recognized species (Gardner 1993), distributed from central Mexico (e. g., *Marmosa mexicana*, Hall 1979) southward to central Argentina and Chile (e. g., *Thylamys*, Tate 1933).

Altitudinally, marmosines range from the lowlands of the Amazon Basin (e. g., *Micoureus*, EMMONS 1990) to elevations as high as 3 500 m in the Andes (*T. pallidior*, TATE 1933). Although the majority of mouse opossums inhabit humid tropical and semitropical forests of the Neotropical region, *Thylamys* seems to be restricted to open areas, and has the southernmost distribution in South America (MANN 1978, Fig. 2). *Thylamys elegans* (Waterhouse, 1839) occurs in the Coastal Desert of Chile and Peru, and the lowlands and middle altitudinal areas of southern Bolivia and northern Argentina. *Thylamys pallidior* (Thomas, 1902) inhabits elevations as high as 3 500 m in the rocky slopes of the Andean Altiplano. *Thylamys pusilla* (Desmarest, 1804) is restricted to the Chaco and Monte Desert regions. *Thylamys macrura* (Olfers, 1818) is restricted to the moist forests of eastern Paraguay, and *Thylamys velutinus* (Wagner, 1842) inhabits the Cerrado of Brazil.

Although the patterns of distribution of marmosines in general, and *Thylamys* in particular, are fairly well known, their systematic relationships are pooly understood. REIG et al. (1987), using morphologic, karyologic, and serologic data, proposed the recognition of *Thylamys* based on TATE's (1933) *elegans* and *microtarsus* groups. Although REIG et al. (1987) did not evaluate relationships within *Thylamys*, they placed this genus as the sister-taxon of the Patagonian opossum *Lestodelphys* and suggested that both were more closely related to the short-tailed opossum *Monodelphis* than to *Marmosa* (sensu stricto) and *Micoureus*. HERSHKOVITZ (1992), using morphological data proposed the new family Marmosidae, comprised of all marmosine genera, as well as *Monodelphis*, *Lestodelphys*, and *Metachirus*. In this new family, HERSHKOVITZ (1992) recognized the subfamilies (among others) Thylamyinae (for *Thylamys*), and Marmosinae (including *Marmosa*, *Marmosops*, *Micoureus*, and *Gracilinanus*). Recent phylogenetic hypotheses based on cytochrome b sequences did not include *Thylamys* (PATTON et al. 1996). KIRSCH and PALMA (1995) using DNA-hybridization proposed *Thylamys* as a differentiated lineage in which *T. pusilla* and *T. macrura* appeared as the most divergent taxa.

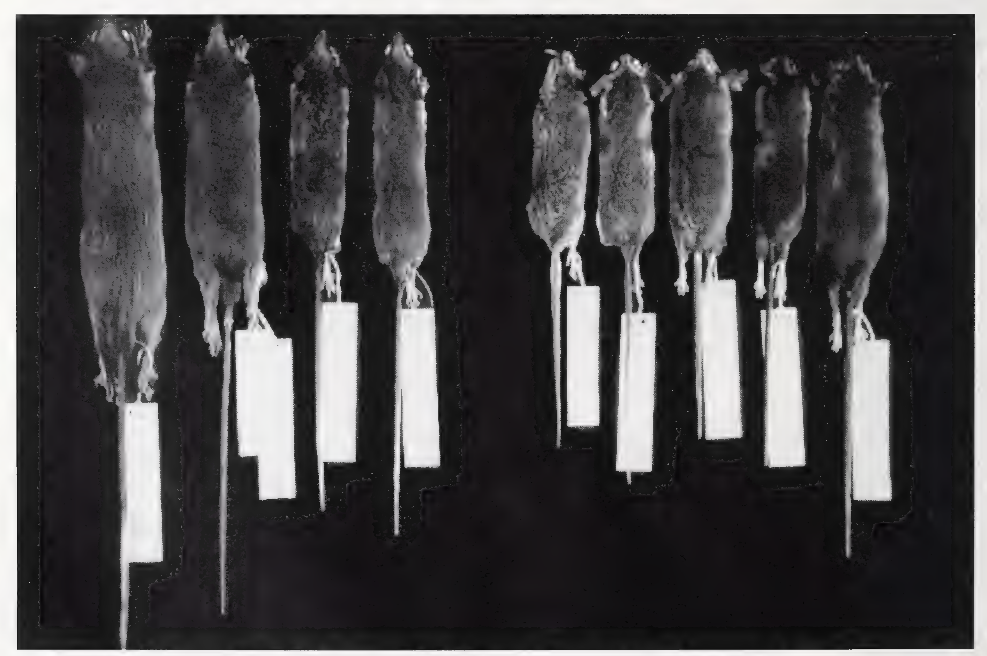


Fig. 1. Dorsal view of skins of mouse opossums (from left to right): *Micoureus cinereus*, *Marmosa robinsoni*, *Marmosops dorothea*, *Gracilinanus agilis*, *Thylamys pallidior*, *T. pusilla*, *T. elegans*, *T. venusta*, and *T. macrura* (total length *T. macrura* = 284 mm).

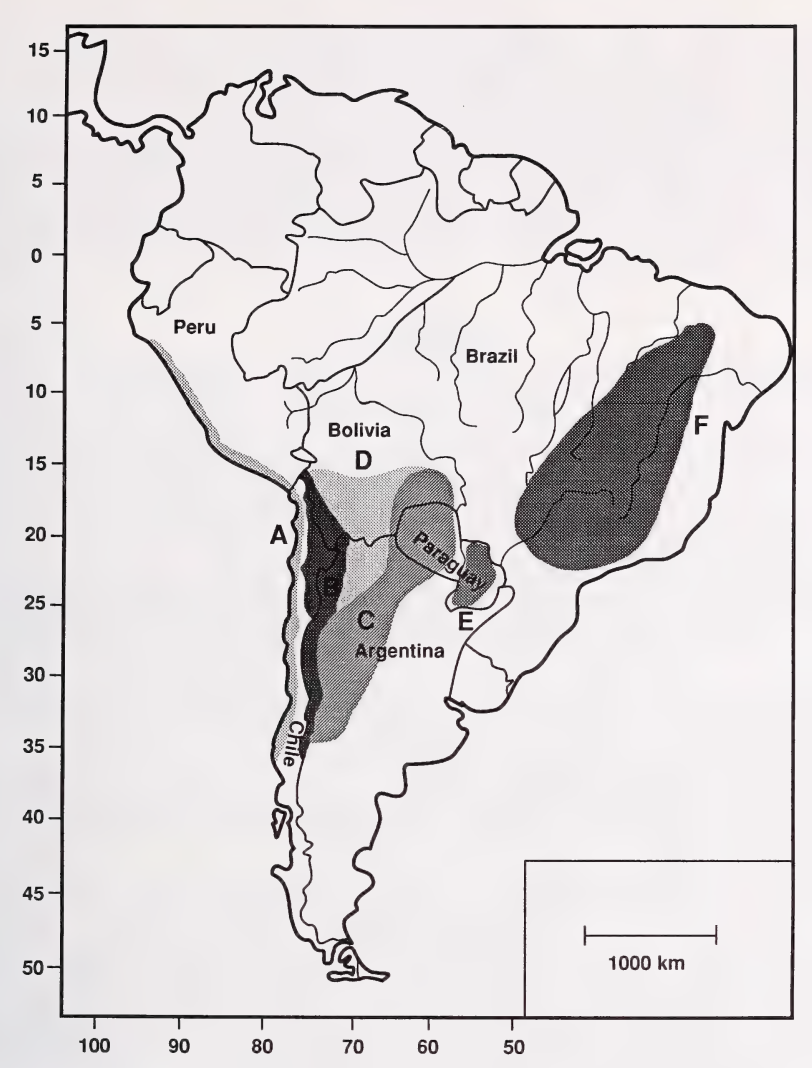


Fig. 2. Ranges of distribution of *Thylamys* in South America. The range of *T. elegans* and *T. venusta* is shown as hypothesized by TATE (1933), and confirmed with the results of this study. A = *Thylamys elegans*, B = *T. pallidior*, C = *T. pusilla*, D = *T. venusta*, E = *T. macrura*, F = *T. velutinus*.

The present study was designed to test the monophyly of *Thylamys* spp., to assess the phylogenetic relationships among *T. elegans*, *T. pallidior*, *T. pusilla*, and *T. macrura*, and to evaluate the relatedness between populations of *T. elegans* across the Andes. The latter objective was focused on TATE's (1933) contention that two species of *Thylamys* were present across the Andean Cordillera, *T. elegans* in the western flank and *T. venusta* in the eastern side, in contrast to CABRERA (1958) who recognized both as *T. elegans*. The systematic relatedness among all taxa was inferred from chromosomes and allozymes. Outgroups included specimens of *Gracilinanus agilis*, *Micoureus cinereus*, *Marmosops dorothea*, and *Monodelphis domestica*.

Material and methods

Chromosomal analyses

Karyotypes were obtained from bone marrow following the conventional Velban technique described by Anderson et al. (1987). Twelve individuals were examined in *Thylamys*, and six from *Gracilinanus*, *Marmosops*, and *Micoureus*. A minimum of 10 metaphase spreads were counted for each specimen. Nomenclature for chromosome morphology and autosomal fundamental number (FN) followed Patton (1967). Chromosomes were arranged sequentially in order of decreasing size, with bi-armed elements preceding single-armed elements.

Allozyme analyses

Horizontal protein electrophoresis was conducted on frozen tissue preparations from 95 specimens of *Thylamys*, of which 77 corresponded to *T. elegans*. Voucher specimens (skins and skeletons) are deposited in the Museum of Southwestern Biology (MSB), Department of Biology, The University of New Mexico, Albuquerque, New Mexico; the American Museum of Natural History (AMNH), New York; Museo Nacional de Historia Natural, La Paz, Bolivia; Museo Noel Keempf Mercado, Santa Cruz, Bolivia; and Museo Nacional de Historia Natural, Asunción, Paraguay. Tissues and cell suspensions are deposited in the Division of Biological Materials of the MSB. Specimens examined were (numbers in parentheses indicate the sample size):

Thylamys elegans, Bolivia: Department of Chuquisaca: Monteagudo (7), Padilla (7), Porvenir (24), Tarabuco (5); Department of Tarija, Tarija (10); Department of Santa Cruz: Vallegrande (8), Quiñe (7).

T. elegans, Chile: Province of Limarí: Fray Jorge (4); Province of Valparaíso: La Campana (5).

T. pusilla, Bolivia: Department of Tarija, Department of Chuquisaca, and Department of Santa Cruz (9).

T. pallidior, Bolivia: Department of Chuquisaca and Department of Tarija (8).

T. macrura, Paraguay: Department of Concepción (1).

Micoureus cinereus, Paraguay: Department of Amambay (1).

M. constantiae, Bolivia: Department of Pando (1).

Monodelphis domestica, Bolivia: Department of Tarija (1); Paraguay: Department of Amambay (1).

Marmosops dorothea: Bolivia: Department of Santa Cruz (1).

Gracilinanus agilis, Bolivia: Department of Santa Cruz (1).

Twenty-one enzymes constituting 26 presumptive loci were examined. These corresponded to: [1] glucose dehydrogenase (GDH), [2] glucose-6-phosphate dehydrogenase (G-6-PDH), [3] hexose-6-phosphate dehydrogenase (H-6-PDH), [4–5] isocytrate dehydrogenase (IDH-2 and IDH-1), [6–7] L-lactate dehydrogenase (LDH-1 and LDH-2), [8–9] malate dehydrogenase (MDH-3 and MDH-1), [10] sorbitol dehydrogenase (SDH), [11] xanthine dehydrogenase (XDH), [12–13] esterases (ES-1 and ES-9), [14] fumarate hydratase (FUMH), [15] octanol dehydrogenase (ODH), [16–17] glutamate oxalate transaminase (GOT-1 and GOT-2), [18] glucose phosphate isomerase (GPI-1), [19] alfa-glycerophosphate dehydrogenase (alfaGPD-1), [20] hexokinase (HK), [21] malic enzyme (ME-1), [22] nucleoside phosphorilase (NP), [23–25] peptidases (PEP-A, PEP-B, and PEP-F), and [26] phosphoglucomutase (PGM-1). An additional protein, alcohol dehydrogenase (ADH), was also assayed, and although it showed polymorphism among populations it could not be scored consistently in all samples. Isozyme systems, stains, and electrophoretic procedures followed Selander et al. (1971), Murphy et al. (1990), and Yates and Greenbaum (1982). Genotypes at each locus were analyzed using the BIOSYS-1 computer program (Swofford and Selander 1981), which computed levels of polymorphism (P), heterozygosity (H), and the degree of population structure (computing Hardy-Weinberg equilibrium and Wright's hierarchical F-statistics (Wright 1965).

Phylogenetic analyses

Allozyme data were analyzed under the principle of maximum parsimony using the computer program PAUP*, version 4.0d52 (Phylogenetic Analysis Using Parsimony, written by David L. Swofford). The allozymic data were analyzed as unordered characters in two ways: first, using the locus as a character, and the allelic combination of the locus as the character-state (Buth 1984); and second, using the allele as a character, and its presence or absence as the state. All equally parsimonious trees were found

through an exhaustive search excluding uninformative characters, and strict and 50% majority-rule consensus trees are presented to summarize the shortest tree lengths. Branch-and-bound bootstrap analyses with 1000 replicates were performed on the data sets to estimate the confidence for each node. Phylogenetic analyses were also accomplished using the Neighbor-Joining algorithm available in PAUP 4.0, and the nodes in the tree were evaluated by a Neighbor-Joining search bootstrap with 1 000 replicates using PAUP. Additionally, the maximum-likelihood technique was implemented on the gene frequencies using the CONTML program in PHYLIP 3.5 c (Felsenstein 1993). Since the allele frequencies among populations of *Thylamys* spp. were highly similar, they were pooled by species in the maximum-likelihood analysis. The same procedure was followed among the outgroup taxa, and is why we refer to these taxa collectively as "marmosines" through this paper.

Results

Chromosomal variation

The autosomal complements among *T. elegans*, *T. macrura*, *T. pallidior*, and *T. pusilla* appeared to be identical in number and morphology with 2 n = 14 and FN = 20 (Fig. 3, Tab. 1; Palma and Yates 1996). The autosomes in these four species consist of three large submetacentric chromosomes (pairs 1–3), a medium-sized metacentric complement (pair 4), and two small acrocentric elements (pairs 5–6). No variation in this pattern was found in any specimen analyzed. The X chromosome is a small acrocentric in *T. elegans* and *T. pallidior*, and a small submetacentric in *T. macrura* and *T. pusilla*. The Y chromosome was absent in males of *T. elegans* (Bolivia) and *T. pallidior* (Figs. 3 b and 3 c).

The autosomes of *Micoureus cinereus* were identical to that of *Thylamys* (2 n = 14, FN = 20). However, *Gracilinanus agilis* and *Marmosops noctivagus* while sharing the 2 n = 14 diploid number differed in fundamental number (FN = 24) from that found in *Thylamys* and *Micoureus*, due to pairs 5 and 6 being submetacentric instead of acrocentric. The X chromosome in *G. agilis* and *M. noctivagus* is a small submetacentric, while the Y in *G. agilis* is a small submetacentric and that in *M. noctivagus* is a tiny dot (Fig. 3 h).

Allozyme variation

Of the 26 analyzed loci, eight (MDH-1, MDH-3, GDH, H-6-PDH, LDH-1, FUM, PEP-F, and PGM-1) were monomorphic in all taxa examined, whereas the other 18 loci exhibited fixed allelic differences between marmosines and thylamyines. Within *Thylamys*, 10 loci were polymorphic (0.99 eriterion): H-6-PDH, IDH-2, LDH-1, ODH, ES-1, GOT-1, alpha-GPD, ME-1, PEP-A, and PEP-B. *Thylamys elegans* (Chile) and *T. pallidior* had fixed differences at four loci (IDH-2, PEP-A, PEP-B, ME-1) relative to *T. elegans* from Bolivia and other thylamyines from Bolivia and Paraguay. *Thylamys elegans* from Chile and *T. pallidior* shared the same alleles although at different frequencies at IDH-2, PEP-A, PEP-B, and ME-1.

The overall percentage of polymorphic loci (P) across all 12 populations of *Thylamys* was 2.88 (0.95 criterion), or 3.84 (0.99 criterion). Mean heterozygosity per locus per population varied between 0 and 0.01. Similar low values of heterozygosity were obtained in Australian dasyurid marsupials where up to 28 loci were examined (Baverstock et al. 1982; Sherwin and Murray 1990 and references therein). For *Thylamys*, values of chi-square goodness-of-fit showed a departure from Hardy-Weinberg expectation at each variable locus per population (1 D.F., $P < 0.05$), varying between 8.229 (ODH; Quiñe) and 47.022 (alpha-GPD, ME-1, ES-1; Porvenir). The mean value of Wright's F-statistic (F_{ST}, the fixation-index of population subdivision) for all variable loci within *Thylamys* was 0.845.

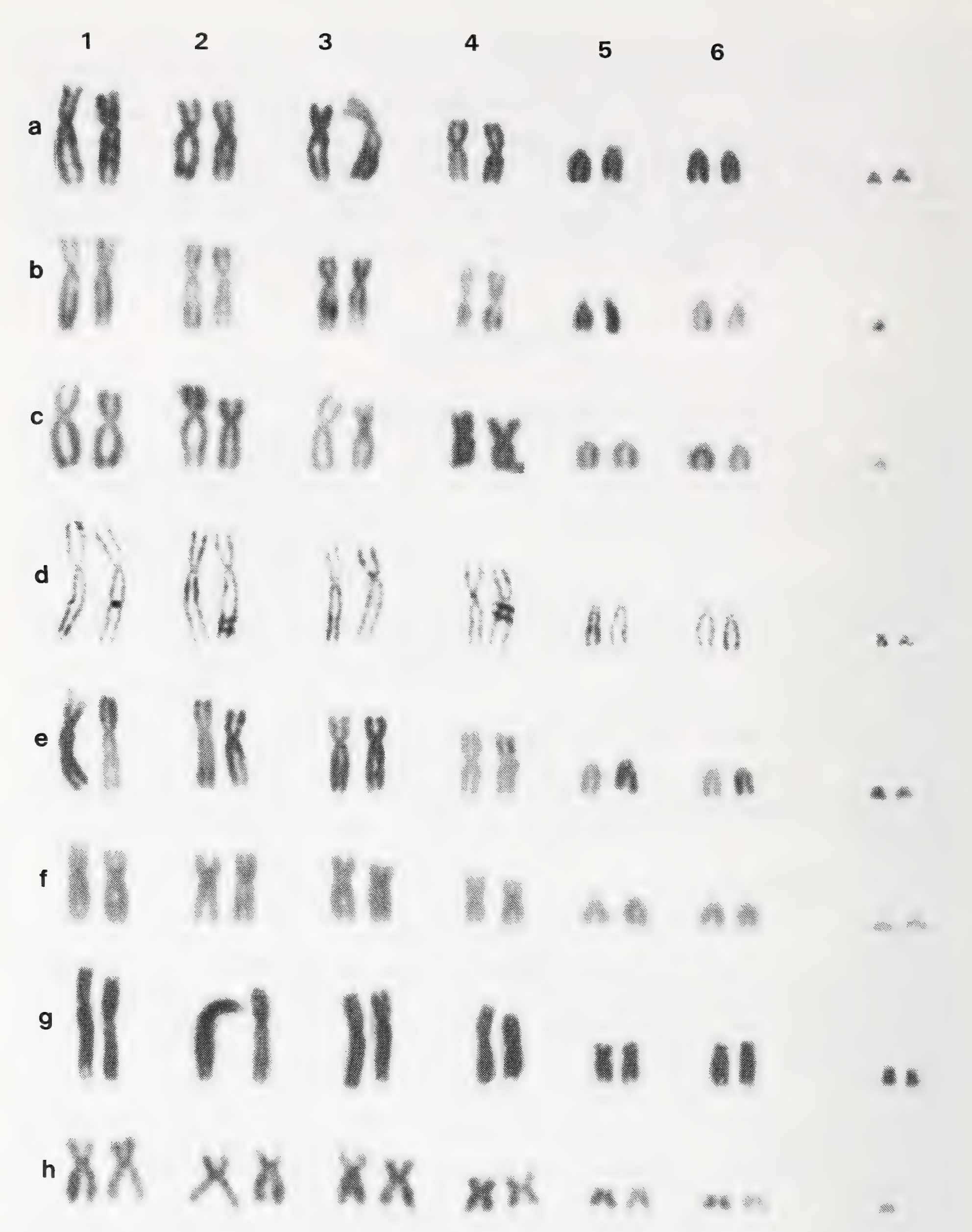


Fig. 3. Standard karyotypes of mouse opossums. The last two chromosomes on each row constitute the sexual chromosomes: a) female *Thylamys elegans* (Chile), b) male *T. elegans* (Bolivia), c) male *T. pallidior*, d) female *T. pusilla*, e) female *T. macrura*, f) female *Micoureus cinereus*, g) female *Gracilinanus agilis*, and h) male *Marmosops noctivagus.*

Parsimony analysis

Locus as a character: Nine equally most-parsimonious trees were obtained through the exhaustive search option of PAUP, all of them 34 steps long, with a consistency index (CI) of 0.941 and a retention index (RI) of 0.933. All rival trees exhibited three polytomous

clades containing *Monodelphis*, *Micoureus*, and the ancestor of a clade that included (*Marmosops-Gracilinanus*)-*Thylamys*. All trees showed *Marmosops* and *Gracilinanus* as the first outgroups to *Thylamys*, and the latter appeared as monophyletic in all most parsimonious trees (Figs. 4 a, 4 b, and 4 c). The bootstrap value for the *Thylamys* clade was

Table 1. Diploid and fundamental number for ten thylamines and marmosines. Abbreviations are 2 N (diploid number), FN (number of autosomal arms), M (metacentric), SM (submetacentric), A (acrocentric), X (X chromosome), and Y (Y chromosome).

Species	2N	FN	M	SM	A	X	Y
Thylamys elegans	14	20	2	6	4	A	–
Thylamys pallidior	14	20	2	6	4	A	–
Thylamys pusilla	14	20	2	6	4	SM	–
Thylamys macrura	14	20	2	6	4	SM	–
Micoureus cinereus	14	20	2	6	4	A	–
Gracilinanus agilis	14	24	2	10	–	SM	SM
Marmosops noctivagus	14	24	2	10	–	SM	–
Marmosops dorothea	14	24	2	10	–	M	A
Marmosa murina	14	24	2	10	–	M	A
Marmosa robinsoni	14	24	2	10	–	M	A

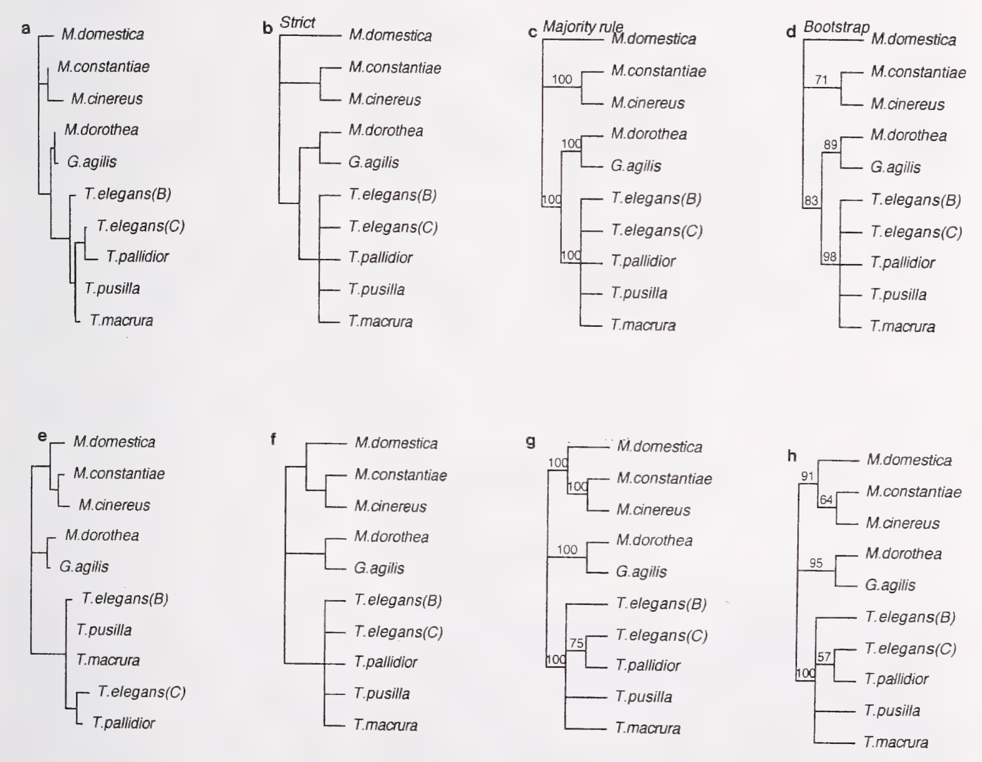


Fig. 4. Allozyme data using the locus as the character (above): a) one of the nine most parsimonious trees showing *T. elegans* from Bolivia as the most basal form, b) strict-consensus tree, c) majority-rule tree d) bootstrap tree. Allozyme data using the allele as a character (below): e) one of the four most-parsimonious trees depicting *T. elegans* from Bolivia as the basal taxon in *Thylamys*, f) strict-consensus tree, g) majority rule tree, h) bootstrap tree. (B = Bolivia, C = Chile).

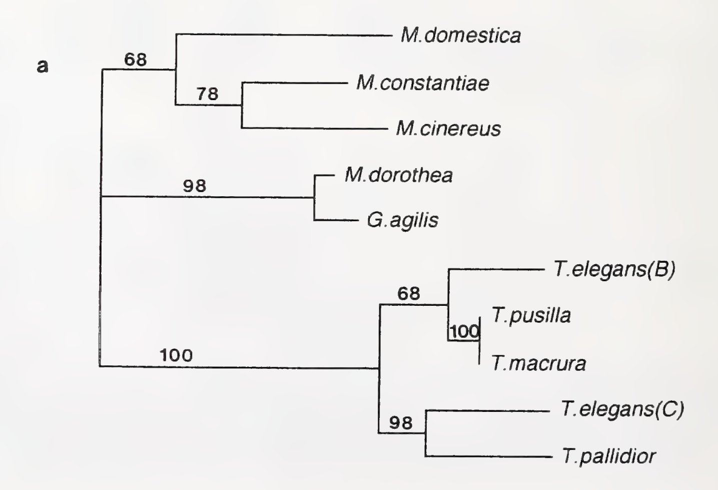
98% (Fig. 4 d). Most of the topologies did not resolve the sequence of phylogenetic relationships within *Thylamys*, particularly the relationships of *T. pusilla* and *T. macrura*. In three reconstructions, *T. pallidior* appeared as the sister-taxon of *T. elegans* from Chile, while the other six rival trees depicted *T. elegans* from Bolivia, *T. elegans* from Chile, and *T. pallidior*, as the most basal thylamyines.

Allele as a character: Four equally most parsimonious trees were obtained using the exhaustive-search option, each 56 steps long with CI = 0.679 and RI = 0.788. Again, as observed in figure 4 e, three polytomous subsets were obtained: the *Monodelphis* clade, the *Micoureus* clade, and the ancestor of a (*Marmosops-Gracilinanus*)-*Thylamys* clade. *Marmosops* and *Gracilinanus* appeared as the sister-group to *Thylamys*, and this association was recovered 100% of the time in the consensus and bootstrap analyses (Figs. 4 f and 4 h). Three out of four trees exhibited *T. elegans* (Chile) as the sister-taxon of *T. pallidior*, as shown by the consensus tree in figure 4 e. The fourth topology showed *T. elegans* (Bolivia) as the sister-group of *T. pallidior*. As with the locus-as-character analysis, the sequence of phylogenetic relationships of *Thylamys* was not completely resolved for *T. macrura* and *T. pusilla*. *Thylamys elegans* (Bolivia) was found to be the most basal form in the majority of topologies.

Distance and likelihood analyses

The Neighbor-Joining tree differentiated mouse opossums in three major subsets: *Monodelphis-Micoureus*, *Marmosops-Gracilinanus*, and *Thylamys* spp. (Figs. 5 a and 5 b). Within *Thylamys*, the grouping between *T. pallidior* and *T. elegans* Chile was recovered 98 and 58 percent of the time in the locus and allele bootstrap analyses, respectively (Figs. 5 a and 5 b). The sister relationship of *T. elegans* from Bolivia and *T. pusilla–T. macrura* was supported 68 and 78 percent of the times in the locus and the bootstrap analyses, respectively. *Thylamys elegans* from Bolivia was the outgroup to the latter two species in both analyses (Figs. 5 a and 5 b).

The topology of the maximum-likelihood tree (28 trees examined, Ln Likelihood = 193.52829) also showed the three major subsets: marmosines, *T. pallidior–T. elegans* (Chile), and *Thylamys* spp. from the eastern Andes (Fig. 6). Furthermore, as recovered with the Neighbor-Joining tree, *T. elegans* from Bolivia appeared as the basal form related to the *T. macrura–T. pusilla* grouping.



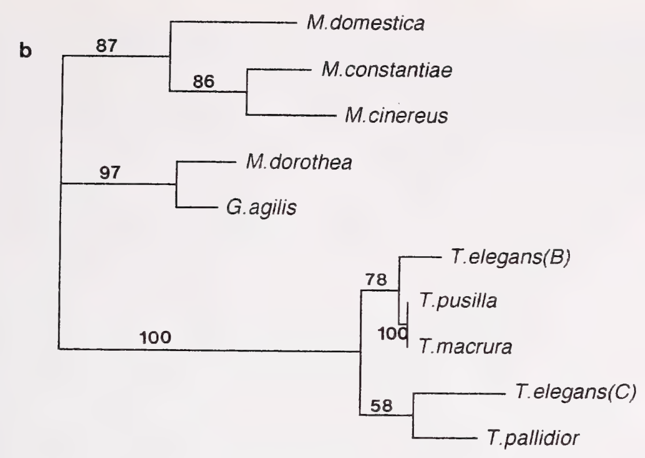


Fig. 5. Neighbor-joining trees based on a) the locus as the character, and b) the allele as the character. Numbers on the nodes represent the 1 000 bootstrap replicate values.

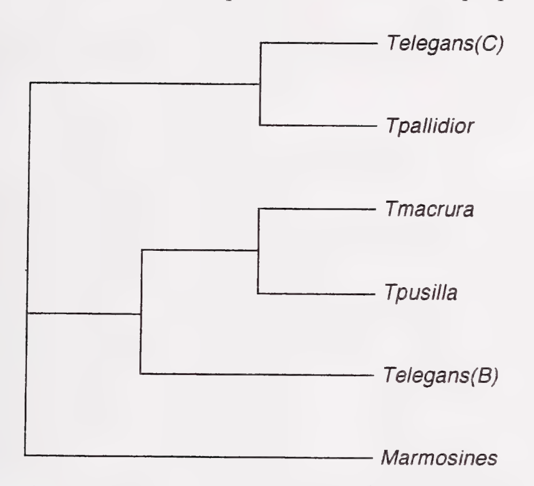


Fig. 6. Maximum-likelihood tree among *Thylamys* spp. (28 trees examined, Ln likelihood = 193.52).

Discussion

Chromosomal analyses

Although marmosine opossums are known for a lack of variation in the total number of chromosomes (2 n = 14; Hayman 1990, although see Engstrom and Gardner 1988), differences are apparent in fundamental number (Reig et al. 1977; Hayman 1990; Palma and Yates 1996). The FN = 20 reported here for *Thylamys* contrasts to the FN = 24 of *Marmosa*, *Marmosops*, and *Gracilinanus*, for example. The karyotype of *Micoureus* presented here, and those obtained from additional localities in Peru and Venezuela (Reig et al. 1977), appear identical to that of *Thylamys*, although these apparent chromosomal affinities should be examined using banding methods. The differences in the number of autosomal arms in mouse opossums are most likely the result of non-Robertsonian changes, such as pericentric inversions which involve changes in the number of autosomal arms but not in the number of chromosomes (Patton and Sherwood 1983).

The morphology of sex chromosomes was found to be highly variable within *Thylamys*. The X chromosomes varied from acrocentric (*T. elegans*) to submetacentric (*T. macrura*). This pattern has also been found in other marmosines (e. g., *Micoureus*, *Gracilinanus*; PALMA and YATES 1996). However, in *T. elegans* (Chile and Bolivia) and *T. pallidior*, the Y chromosome was not observed (PALMA 1995 a), whereas in *M. noctivagus* it was dot-like as detected in the aquatic opossum *Chironectes minimus* (PALMA and YATES 1996).

The apparent lack of an obvious Y chromosome is difficult to verify with the methods followed in this study. It is possible that the Y has been translocated to another chromosome, or this condition may be another example of chromosome mosaicism, i. e. a difference in sex-chromosome composition between the germ line and cells of the somatic tissues (HAYMAN 1990). This phenomenon has also been detected in other marsupial taxa, such as in the Chilean microbiotheriid *Dromiciops gliroides* (GALLARDO and PATTERSON 1987), and in some taxa of the Australasian families Pseudocheridae and Peramelidae (HAYMAN 1990). The missing Y chromosome in *Dromiciops* eaused GALLARDO and PATTERSON (1987) to hypothesize that *Dromiciops* may be more closely related to Australian than to American marsupials, supporting SZALAY's (1982) contention that *Dromiciops* and Australian metatherians constitute the cohort Australidelphia. Data from this study and from PALMA and YATES (1996) suggest that sex chromosome mosaicism may be found not only in *Dromiciops* and Australian metatherians, but in other American marsupials as well. If true, this evidence provides a typical case of parallelism in the evolution of metatherian sexual chromosomes.

Allozyme analyses

Allozyme data using parsimony, distance, and likelihood analyses consistently supported a monophyletic association among *Thylamys* spp. distinct from other opossums. These results agree with those obtained through chromosomal and DNA-hybridization methods (KIRSCH and PALMA 1995) that recognized *Thylamys* as a differentiated lineage with respect to other small didelphids. Consequently, *Thylamys* should be recognized as a monophyletic assemblage, and as a valid genus. Earlier morphologic studies also recognized thylamyines at the generic level (REIG et al. 1987), although these authors included TATE's *microtarsus* group in *Thylamys* instead of in the genus *Gracilinanus* (GARDNER and CREIGHTON 1989). Therefore, the hypothesis that *Gracilinanus* is a member of a lineage distinct from *Thylamys* (GARDNER and CREIGHTON 1989) is supported by the results of this and from DNA-hybridization studies (KIRSCH and PALMA 1995).

Allozyme parsimony using the locus as the character showed that *Marmosops* and *Gracilinanus* constitute the sister-group to *Thylamys*, concurring with DNA-hybridization studies (KIRSCH and PALMA 1995). These and other results allowed KIRSCH and PALMA (1995) to propose the subfamilies Thylamyinae (with the tribes Thylamyini and Marmosopsini; the latter including *Marmosops* and *Gracilinanus*), the Marmosinae (consisting of Marmosini; for *Marmosa* and *Micoureus*), and Monodelphini (for *Monodelphis*; KIRSCH, and PALMA 1995). This classification proved to be consistent with the three clades obtained with allozyme parsimony, although the analysis did not include the genus *Marmosa*. PATTON et al. (1996) also found, that *Marmosops* was excluded from a clade containing *Marmosa*, *Micoureus*, and *Monodelphis* based on phylogenetic analyses of cytochrome b sequences. Although we did not evaluate the relationships between small-bodied versus large marsupials, the recognition of mouse opossums as a family including *Metachirus* (Marmosidae; HERSHKOVITZ 1992) has found no support through molecular analyses using DNA-hybridization and cytochrome b methodologies (KIRSCH and PALMA 1995; PATTON et al. 1996).

Allozyme distance and likelihood analyses suggests that a major historical biogeographic event (e. g., vicariance) may have triggered the differentiation of *Thylamys* across

the Andes, giving rise to western and eastern forms. This historical scenario may have allowed the speciation of *T. pallidior* in the Prepuna and Puna areas of the Andes, and of *T. elegans* in the western lowlands and Coastal Cordillera of Chile and Perú, leaving *T. elegans* (Bolivia), *T. pusilla*, and *T. macrura* at the eastern side of the Andes. The populations of *T. elegans* from Chile differed by fixed differences at four enzymatic loci with respect to eastern populations of *Thylamys* spp. These fixed allele differences were also shared by populations of *T. pallidior*, although at different frequencies. The high F_{ST} value obtained in this study suggests that strong genetic differentiation has occurred within *Thylamys* as evidenced by the fixed loci that differentiated populations across the Andes, and the low values of heterozygosity on either side of the Cordillera. The F_{ST} value also shows that thylamyine populations as a whole are not in Hardy-Weinberg equilibrium, indicating that populations are either not randomly mating, and/or some evolutionary force may be acting within populations. The low values of polymorphism and heterozygosity suggest that gene flow might be maintaining the genetic homogeneity among populations on either side of the mountains. Alternatively, the extremely low values of genetic heterozygosity and deviations from the Hardy-Weinberg expectations within *Thylamys*, would imply that some populations of the most basal species may have experienced one or more recent severe bottlenecks. The latter may have been triggered by geological events during the Plio-Pleistocene in the Andes and surrounding areas, during the great uplift of the Cordillera and/or the glacial periods (Potts and Behrensmeyer 1992). Although we cannot infer the most basal form from distance and likelihood analyses, allozyme parsimony suggests that *T. elegans* from Bolivia might be that form, and it should exhibit the higher levels of genetic variability than all of their descendants (Barton 1989; Avise 1993). Although this has not been found to be the case, the complete range of *T. elegans* in the eastern Andes has not been sampled in term of genetic variation, since the species is also distributed southward to the Argentinean Patagonia (where the oldest fossil records of *Thylamys* have been obtained; Reig et al. 1987). Concurring with allozyme parsimony, preliminary results based on cytochrome b sequences support *T. venusta* as the most basal form (Palma 1994), contrary to what DNA-hybridization studies might suggest (that the basal stock of *Thylamys* would be constituted by *T. macrura* along with *T. pusilla*). We think that the completion of sequencing analyses on the genus will help to clarify this disagreement.

Data from our study are consistent with Tate's (1933) suggestion that *T. elegans* on either side of the Andes mountains represent two distinct species. Thomas (1902) considered the Bolivian form as a subspecies of *elegans* (*Marmosa elegans venusta*). Later, Tate (1933) assigned it specific status naming it *Marmosa venusta* with the subspecies *venusta*, *sponsoria*, and *cinderella*. However, Cabrera (1958) recognized all these forms as subspecies of *T. elegans* from Chile. Therefore, our results support the recognition of two species of *Thylamys* across the Andean Cordillera, *T. elegans* (Waterhouse, 1839) on the western side, and *T. venusta* (Thomas, 1902) on the eastern side. Whether the differentiation of *Thylamys* across the Andes has been due to vicariance, dispersal, or some other historical biogeographic event, cannot be determined until the sequence of phylogenetic relationships among all thylamyines is understood.

Hypothesized relationships through parsimony place the Andean *T. pallidior* with *T. elegans* from Chile as sister taxa when using the allele as the character. Even, when data were analyzed using the locus-as-character, this reconstruction was obtained in three out of nine rival trees. The neighbor-joining and maximum-likelihood analyses also recovered the *T. pallidior–T. elegans* association, and the bootstrap analysis gave high support to this grouping. The occurrence of a recent common ancestor in the evolution of *T. elegans* from Chile and *T. pallidior* is evidenced by the four alleles that both forms share and that differentiate them from other thylamyine taxa. The phylogenetic relationships between the latter two taxa may be interpreted in light of the biogeographic distri-

bution of *T. elegans* and *T. pallidior*. Recent studies have shown *T. pallidior* occurring not only over the western flank of the northern Chilean Andes, but also over the western flank of the Cordillera in northern Chile, and nearby Coastal areas of the latter country where *T. elegans* is found (Palma 1995 b). Alternatively, other topologies in the locus analysis showed *T. pallidior* to be more phylogenetically related to *T. elegans* from Bolivia, as did studies using DNA-hybridization (Kirsch and Palma 1995). This relatedness is consistent with the biogeographic history between the Andes and the Chaco (Potts and Behrensmeyer 1992). Older biogeographic scenarios involve the expansion and contractions of areas during the multiple Pleistocenic glaciations of the Andes, which may have allowed contact between the Andean and eastern Chacoan biota, as hypothesized for the evolution of sigmodontine rodents inhabiting both regions (Mares et al. 1985; Braun 1993).

The parsimony analyses were unable to resolve the phylogenetic relationships within *Thylamys* with respect the placement of *T. macrura* and *T. pusilla* within the clade. This result was obtained when using the locus and the allele as a character, and whether including or excluding *Monodelphis* and *Micoureus* as outgroups. However, distance and likelihood analyses showed *T. pusilla* along with *T. macrura* as sister taxa, while *T. venusta* appeared as the first outgroup to this association. This genetic differentiation may be based on the distributional pattern of the former two taxa, since *T. pusilla* is a form mainly restricted to the Chaco region, while *T. macrura* occurs in the subtropical humid forests, east to the Chaco, suggesting that vicariance would account for the evolution of these forms in both vegetational zones. However, although the main geographic barrier that divides both regions is the Paraguay River, this has not been considered an effective barrier to gene flow, since the river is moderately broad and slow moving in some areas (Myers 1982). Former studies comparing several species of sigmodontine rodents of the Chaco and eastern Paraguay have concluded that the fauna of these regions have diverged due to the abrupt habitat, soil, and topography changes between these areas (Myers 1982). These factors, coupled with dispersal of faunal elements into the Chaco and the Eastern Paraguayan Forests may explain the differentiation of taxa in both vegetational zones (Myers 1982).

At the time of this research it was still believed that *T. velutinus* was "of rare occurrence" (restricted to the Atlantic Forests of Brazil), and this is the reason why this species was not included in the analyses. However, recent studies have shown that *T. velutinus* might not be as "rare" as previously believed, being now also known from the Brazilian Cerrado (Palma 1995 b). Consequently, the results of this study support the recognition of *Thylamys pusilla* (Desmarest, 1804), *Thylamys macrura* (Olfers, 1818), *Thylamys elegans* (Waterhouse, 1839), *Thylamys pallidior* (Thomas, 1902), and *Thylamys venusta* (Thomas, 1902), but is unable to address the status of *T. velutinus.*

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Zusammenfassung

Phylogenie von südamerikanischen Beutelmäusen (Thylamys, Didelphidae) auf der Grundlage von Allozym- und Chromosomendaten

Die phylogenetischen Beziehungen zwischen vier der fünf anerkannten Arten der Gattung *Thylamys* wurden mittels Allozymelektrophorese (26 loci) und Standardkaryotypen untersucht. Die Allozymdaten wurden mittels Parsimonie-, Distanz- und Maximum-Likelihood-Methoden ausgewertet. Bei allen untersuchten Taxa waren die Diploidieverhältnisse und die Chromosomenzahl konstant ($2n = 14$, FN = 20). Die FN unterschied sich jedoch von jener anderer kleiner Opossumformen durch FN = 24. Die verschiedenen konstruierten Stammbäume bestätigten die Abgrenzung von *Thylamys* gegenüber anderen neotropischen Mausopossums als eine monophyletische Gruppe. Das Vorkommen von *T. elegans* sowohl auf der westlichen als auch auf der östlichen Seite der Anden wurde durch unsere Allozymdaten nicht bestätigt. Dies stützt die Behauptung von TATE (1933), daß hier zwei unterschiedliche Arten vorhanden sind. Andere Ergebnisse der Stammbaumanalysen ergaben eine gewisse Verwandtschaft von *T. pallidior* mit *T. elegans* von der chilenischen Westseite der Anden, während *T. elegans* aus Bolivien als die ursprünglichste Form der Thylamyinen zu interpretieren war. Nach unseren Befunden sollte die letztere Form vielleicht als eigene Art, *T. venusta*, anerkannt werden.

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The Red fox in Norway: Morphological adaptation or random variation in size?

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Abstract

Lund (1959) collected red foxes *Vulpes vulpes* from different sites in Norway. We reanalysed his data on body mass, body length, tail length and condition in an attempt to study some factors influencing size variation in foxes. Sexual dimorphism was most significant, with regional variation followed by yearly and seasonal variation. Males were larger (4–5%) and heavier (14%) than females, but not in better condition. Foxes increased in size from south to mid Norway, but were smallest in north Norway. Sexual dimorphism in mass decreased progressively from south to north. Yearly variation was greatest in males. Both males and females were in better condition during autumn and winter, and in poorer condition in the spring. Seasonal changes in mass were similar, but less systematic. Environmental factors that change most from south/mid Norway to north Norway are climatic with lower temperatures, longer winters and lower primary productivity to the north. A smaller northern fox may need a shorter period of growth and conserve energy during the winter.

Key words: Size variation, environmental factors, *Vulpes*

Introduction

The red fox *Vulpes vulpes* is a highly adaptable carnivore, distributed throughout most of the northern hemisphere. Local and large scale variation in size have been found (e.g., Davis 1977; Kolb 1978; Dayan et al. 1989; Huson and Page 1980; Lüps and Wandler 1983), last summarized by Cavallini (1995). Although finding both increased mass, head and body length, and tail length with latitude, Cavallini (1995) concluded that body size reflected phylogenetic distance more than ecological conditions. Geographical variation in size has also been found in other fox species, e.g. arctic foxes *Alopex lagopus* (Frafjord 1993 a), Blanford's foxes *Vulpes cana* (Geffen et al. 1992) and Chilean foxes *Dusicyon* sp. (Fuentes and Jaksic 1979), but none of these supported Bergmann's rule. Bergmann's rule that "races from cooler climates tend to be larger" has been much debated (e.g., Kolb 1978; Cluton-Brock and Harvey 1983, Geist 1987; Dayan et al. 1989). Even in cases where a positive relationship between body size and latitude has been found, other explanations were sought (e.g., Cavallini 1995). As pointed out by Clutton-Brock and Harvey (1983), although relative surface area is smaller in large animals, absolute surface area is larger, and a larger animal will not save energy in absolute terms. Alternative explanations for the red fox include population density, interspecific competition, size of prey, type of prey, the length of the dark winter night, and productivity of the area.

Norway stretches through 13 degrees of latitude, from 58° to 71° N. Generally, the climate is colder with longer winters towards the north (the northernmost part being subarctic), which implies a lower productivity and a shorter growing season. In north Norway

the midnight sun shines during May–July. The red fox is found throughout Norway, in a wide variety of habitats and climatic regimes. According to Lund (1962) it preys primarily on small rodents, hares, and birds. Carcasses of larger mammals may be an important source of food during the winter. Regional variation in prey type and size is most likely small. The terrestrial fauna is similar from south to north, but there are some small variations. For instance, wood mice *Apodemus* sp. are absent in north Norway (Lura et al. 1995), and carcasses of domestic reindeer *Rangifer tarandus* are more available in the north. The importance of vegetable matter in the diet of the Norwegian red fox is unknown.

This study presents analyses of size variations in the Norwegian red fox, attempting to find some of the sources of variation.

Material and methods

All the data came from Lund (1959), who examined red fox carcasses collected from hunters, the largest sample in Norway. Lund (1959) presented data on body size, mass, condition and sex ratio and compared them to reports in the literature. He provided only averages and minima and maxima, and made no statistical analysis in those pre-computer times. Fortunately, he also presented all the original data in a table, which we recalculated to verify some of his conclusions and to look further into some sources of variation. All our analyses and presentations are different from those of Lund (1959), except that we also include our averages for comparison.

Lund (1959) included capture site, date, age (adult or juvenile), sex, mass, total length, tail length (excluding tail hairs), and condition. We pooled capture site by county, used only adult-sized foxes (from October, n = 348) and calculated body length as total length minus tail length. Condition was given as a "fat index", based on the amount of subcutaneous and visceral fat (Lund 1959): 1 very fat, 2 fat, 3 lean, 4 very lean. Most foxes (n = 293, 84.4%) came from only six counties in three regions (Fig. 1): Akershus and Telemark (south Norway), Sør-Trøndelag and Nord-Trøndelag (mid Norway), and Troms and Finnmark (north Norway). Foxes were collected during 1950–1956. In all regions there are large altitudinal gradients in vegetation and fauna, but most red foxes were probably caught in lowland, forested regions.

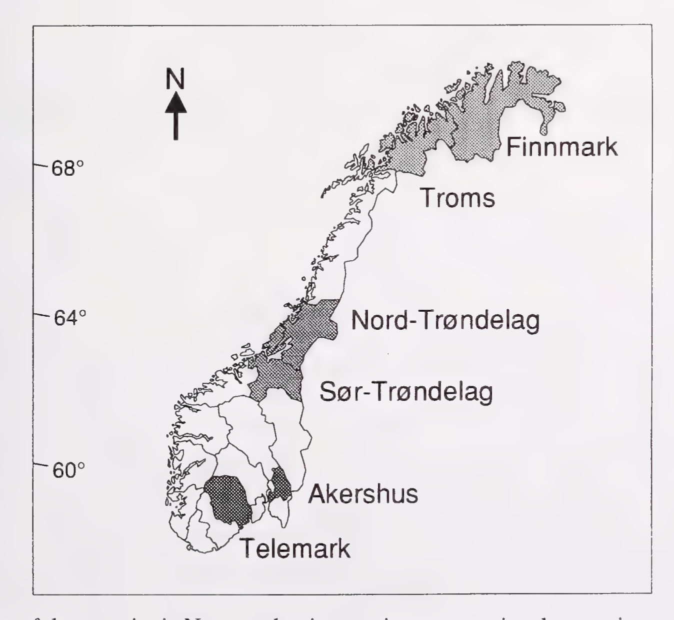


Fig. 1. Map of the counties in Norway, the six counties representing three regions are outlined.

Mass, body length and tail length were normally distributed, but condition was not (K–S Lilliefors tests). We used parametric tests (Student's t-test, ANOVA with Scheffé multiple comparison test) for normal variables and the Mann-Whitney U-test (z score) and Kruskal-Wallis one-way ANOVA (κ^2) for condition. All tests were two-tailed. We include the entire samples in the figures, but in statistical analysis and conclusions only groups with more than 10 foxes are used.

Results

Males were significantly heavier (14%) and larger (4–5%) than females, but not in better condition (Tab. 1). Sexual dimorphism in mass was about three times larger than in length. The three measurements mass, body length and tail length were significantly correlated with each other, as was also the condition index except with tail length (Tab. 2). Our results are slightly different from those of Lund (1959), possibly because we used a slightly smaller sample size.

Table 1. Mean mass, body length, tail length and condition of male and female red foxes, the ratio of male/female (R), and test between the sexes.

	Males			Females					
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	R	t	p
Mass (g)	5 887	962	192	5 186	948	155	1.14	6.79	<0.001
Body length (cm)	68.6	3.6	188	65.8	3.9	154	1.04	6.82	<0.001
Tail length (cm)	43.8	3.0	188	41.8	3.0	154	1.05	5.97	<0.001
Condition index	2.90	0.6	185	2.88	0.7	149	1.01	0.30	>0.05*

* Mann-Whitney U-test

Table 2. Pearson's correlations between mass, body length, tail length and condition in the red foxes (minimum pairwise n = 328). ** = p < 0.001.

	Mass	Body length	Tail length
Body length	0.64**		
Tail length	0.45**	0.37**	
Condition	0.49**	0.19**	0.06

The general pattern of regional variation was similar for mass, body length, tail length and condition (Fig. 2). Within sexes, significant variation between counties was found for male body mass. Males from Finnmark were lighter than those from Nord-Trøndelag, Sør-Trøndelag and Akershus (F = 7.03, d. f. = 5,155, p < 0.001, Scheffé test).

Combining the 6 counties into 3 regions, an overall tendency of larger foxes in mid Norway and smaller foxes in north Norway becomes clearer. Northern males were lighter (F = 12.7), and had shorter body length (F = 5.7) and tail length (F = 7.2) than males from mid Norway, and were lighter than males from south Norway. Northern females were lighter (F = 3.3) and had shorter tails (F = 7.2) than females from mid Norway, and females from south Norway had shorter tails than those from mid Norway. A similar overall regional variation was also found for female body length (F = 3.3), but no two regions were significantly different from each other. Regional variation was also found in male

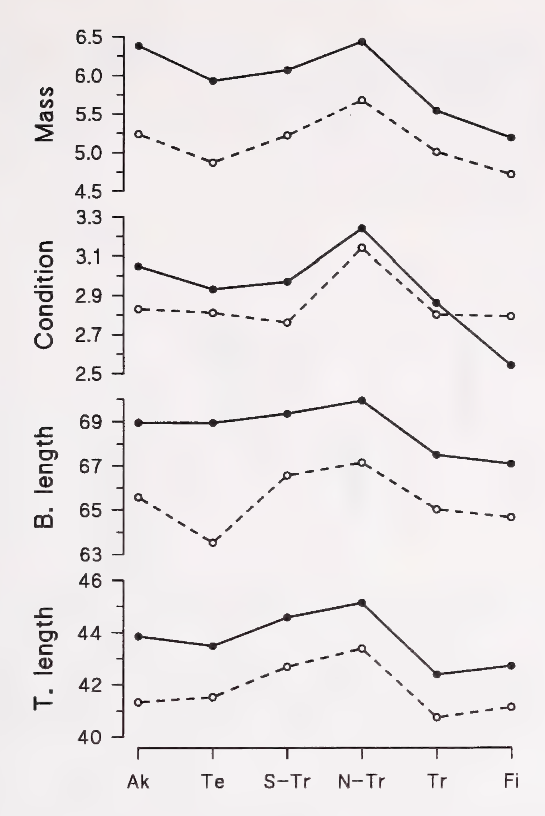


Fig. 2. Average mass (kg), condition index, body length (cm), and tail length (cm) of male (●) and female (○) red foxes from six counties (Ak-Akershus, Te-Telemark, S-Tr-Sør-Trøndelag, N-Tr-Nord-Trøndelag, Tr-Troms, and Fi-Finnmark).

condition ($\kappa^2 = 11.77$, $p < 0.01$). If males vary more than females, one might expect a reduced sexual dimorphism northwards. This was most pronounced in mass (male/female ratio 1.17, 1.14 and 1.09 for south, mid and north Norway) and less in condition, body length or tail length.

Yearly variation in mass and size through 1950–1956 was most pronounced in males (Fig. 3). Most foxes were caught in the years 1951 to 1954. We excluded the years 1950 and 1955–1956 from the analyses of yearly variation, using only 1951–1954 so that no group (by year by sex) contained less than 16 foxes. No significant yearly variation was found in female mass, body length or tail length. Males, on the other hand, were particularly small in 1954, being lighter ($F = 7.7$) with shorter tails ($F = 4.9$) than in 1951 and 1952, and smaller body length ($F = 3.5$) than in 1952. Yearly variation in condition was also found in males ($\kappa^2 = 13.89$, $p < 0.01$, Fig. 3).

No seasonal differences were found in body mass for either males or females, although values were nearly significant (males: $F = 3.2$, d.f. = 3,188, $p = 0.06$, females: $F = 2.4$, d.f. = 3,151, $p = 0.07$). Seasonal differences were found in male condition ($\kappa^2 = 16.06$, $p = 0.001$), but not in female condition. Males were in poor condition in the spring (2.56 ± 0.63, n = 41) and in best condition in the autumn (3.08 ± 0.64, n = 66).

The data were split into groups by the two sexes, three regions, and four seasons. For each group, mass and condition were calculated as percent deviation from the average within the group. Sample sizes were notably small and inconclusive for the summer sea-

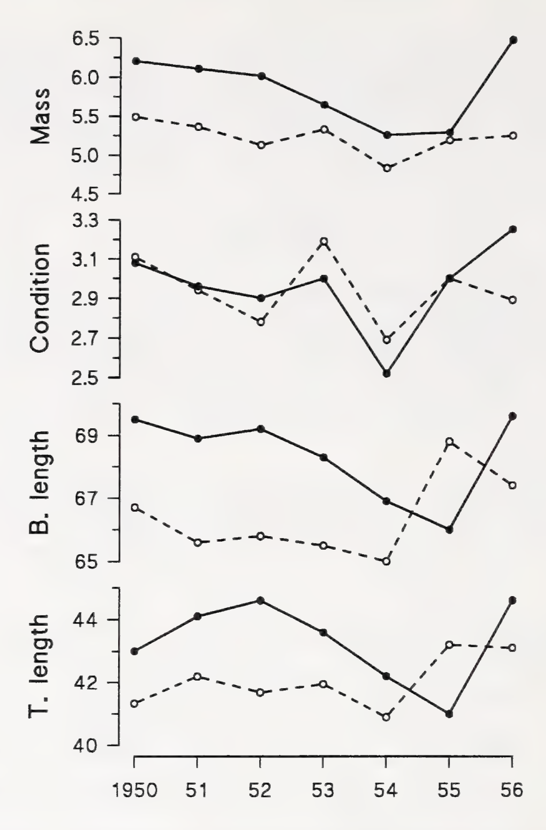


Fig. 3. Average mass, condition index, body length, and tail length of male (●) and female (○) red foxes through different years.

son (Fig. 4). Males were heaviest in the winter in all regions and in north Norway in the autumn (Fig. 4). Female mass appeared to vary less systematically, but females in south Norway were notably light in winter and heavier in spring and autumn (Fig. 4). To some extent, a similar pattern was found for the condition index, with foxes in better condition in autumn and winter and in poorer condition in spring (Fig. 5). The patterns for males and females were more similar for condition than for mass.

The data were not evenly distributed. Of the 82 foxes collected in north Norway, 96.3% were collected in 1953 and 1954. In mid Norway, 89.2% of the 111 foxes were collected in 1951 and 1952. In south Norway, 63.1% of 149 foxes were collected in 1951 and 1952. Thus, more of the smaller foxes in north Norway were collected in what may have been "bad" years for the red fox, implying that regional variation may be somewhat obscured or exaggerated by the effect of yearly variation. In an ANOVA of mass with sex, region, year and season as independent variables, only sex had a significant influence ($F = 42.4$, $F = 2.1$, $F = 0.7$, and $F = 1.3$, respectively). No two-way interactions of these factors were significant for mass.

For males and females we calculated the ratio maximum/minimum for each group (Tab. 3). The ratios of mass and condition were about three times higher than the ratios for body and tail lengths, i. e. the variation in the four measurements were proportional. In some cases, females of the largest group were larger than males of the smallest group. Male ratios averaged ± SD 1.09 ± 0.08 and female ratios 1.07 ± 0.05 ($z = 0.06$, $p > 0.05$).

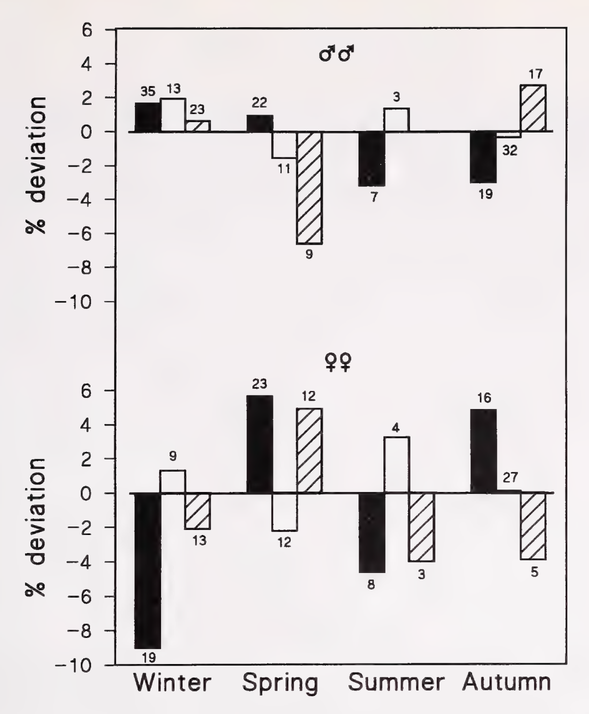


Fig. 4. Average seasonal deviations from the mean mass in male and female red foxes in south Norway ■, mid Norway □, and north Norway ▨: Numbers represent sample size. Winter = December–February, Spring = March–May, Summer = June–August, Autumn = September–November.

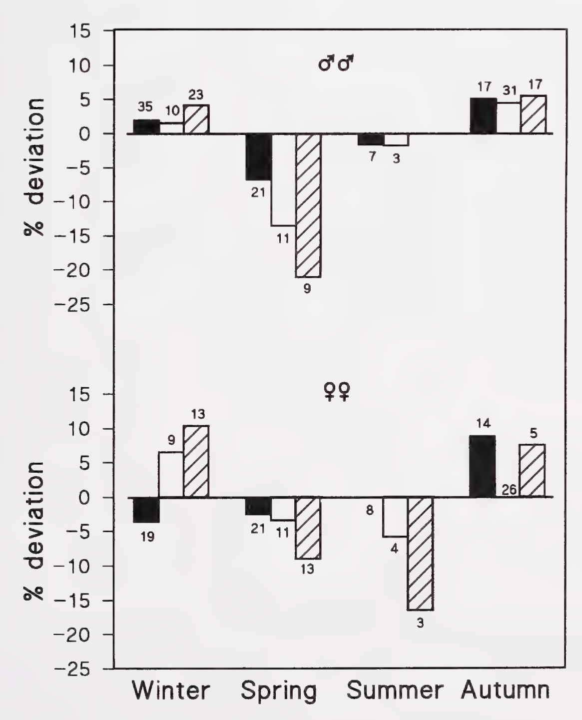


Fig. 5. Average seasonal deviations from the mean condition in male and female red foxes in south Norway ■, mid Norway □, and north Norway ▨: Numbers represent sample size. Seasons as in Fig. 4.

Table 3. The ratio maximum/minimum in each group of male (n = 162–192) and female (n = 126–155) red foxes from three regions, four years (1951–1954) and four seasons.

	Mass	B. length	T. length	Condition
		Males		
Regions	1.16	1.03	1.03	1.14
Years	1.16	1.03	1.06	1.19
Seasons	1.02	1.02	1.01	1.20
		Females		
Regions	1.11	1.03	1.05	1.05
Years	1.11	1.01	1.03	1.19
Seasons	1.10	1.03	1.06	1.10
Average all	1.11	1.03	1.04	1.15

Discussion

The abundance, distribution, and type of food have often been cited as determinants of behaviour and social organization in red foxes (e. g., Macdonald 1981; Lindström 1986; Cavallini and Lovari 1991). Relationships between home range size and metabolic needs have been found in carnivores (Gittleman and Harvey 1982), as well as between body size and behaviour in canids (Bekoff et al. 1981). Harris and Steudel (1997) found that prey-capture behaviour affected the evolution of carnivore hind-limb length most, and that home range size, daily distance moved, prey size, and latitude were less important. In long-legged carnivores, like the red fox, stalking with pouncing or chasing predominates (Harris and Steudel 1997). The red fox probably uses this method when hunting most vertebrate prey species, but it may be most crucial when hunting small mammals (voles and hares). A possible relationship between red fox size and the proportion of vertebrates in the diet has not been examined. In Wales, Huson and Page (1980) related geographical variation in size to some unknown ecological factor, and altitude was suggested as a possible factor. Kolb (1978) found that foxes in Scotland grew larger from south to north, and the most important factor was suggested to be the length of the winter night rather than climate, prey size or productivity of the area. Dayan et al. (1989) suggested that competition with other canids could influence size variation in foxes through character displacement. Within central Italy, Cavallini (1995) found smaller foxes in the south than in the north. This was attributed to a higher density of foxes in the south, and not to food supply or climate because the variation in these factors was small. Cavallini (1995) suggested that the similar result of Kolb (1978) in Scotland may also be explained by population density. On the larger scale of Europe and North America Cavallini (1995) suggested that phylogenetic distance was more important than ecological conditions to explain an increase in body mass and length with latitude.

We ordered the proximate factors into three groups. 1) Environmental factors: latitude/climate, length of the winter, length of snow cower, snow depth, length of the winter night, altitude, interspecific competition. 2) Prey availability: prey type, productivity/food abundance, proportion of vertebrates in the diet. 3) Intrinsic factors: population density, behaviour, social organization. Which factors influence the size of the Norwegian red fox most? Climate, length of the winter, and primary productivity are most likely to be the factors that differ most within south, mid, and north Norway. As conditions deteriorate to the north Norway, foxes most likely experience a cooler climate, a longer winter and a re-

duced food supply. The reduced size and mass are then means of reducing energetic costs (Mcnab 1980), possibly also resulting in a reduced period of growth. This fits well with what has been found in the arctic fox (Frafjord 1993 a) and in the common shrew *Sorex araneus* (Frafjord et al. 1994). Energetic constraints may possibly also reduce population density, but the influence of density on size is uncertain. A high density may reduce the amount of food per fox and select for small foxes, but a high density may also increase competition and select for more competitive and larger foxes. Hersteinsson and Macdonald (1992) suggested that the northern limit of the red fox is determined by resource availability, a theory that was supported by our study.

Lower temperatures or higher latitudes have been associated with greater body mass in the red fox (Dayan et al. 1989), but the determinants of the variation may be complex (Cavallini 1995). There may be a threshold level of temperature or latitude below or above which size cannot increase because of the overall lower productivity further north. This may explain the increase in red fox size from south to mid Norway, and the smaller size of foxes in north Norway (including a reduced sexual dimorphism in the north). Thus, the size of the red fox may follow Bergman's rule in the southern part, with climate as an indirect factor, but not in the north (sensu Geist 1987). It would have been interesting to know whether limb length is proportional to body length in the three regions, or relatively larger in north Norway. A shortening of limbs has been associated with adaptation to a cooler climate, acting independent of body length. An effect against a shortening of limbs is perhaps snow depth. Because tail length was proportional to body length in the three regions, such any adaptation is unlikely.

Males varied in size and mass more than females both between regions, between years and between seasons. It was difficult to separate the effects of these three variables, and some bias was possibly due to different sampling among regions and years. The vole cycles are not synchronised throughout Norway (Christiansen 1983), so a bad year with few voles in one region may be a good year with many voles in another region. The amount of variation in the size of the red fox is similar to that found within other countries (including a study of Norwegian red fox skulls, Frafjord 1993 b), but smaller than between countries (Cavallini 1995). Larger variation in males may indicate greater environmental influence on the size of the larger sex. Seasonal variation in mass and condition are also related to differential energy expenditure in reproduction by males and females. Males use more energy early, i. e. in late winter and spring, when they defend territories most intensively. Females use most energy in late spring and summer, in the final stages of pregnancy and during lactation and feeding of pups. This was partly indicated by the data, with both males and females being in poor condition in the spring. Reproduction may possibly start 1–2 months earlier in south Norway than in north Norway.

Body mass of the red fox may vary as much as 75% between populations, and length 24% (from Cavallini 1995). The red fox in Norway is of medium size, but of comparatively smaller mass (Cavallini 1995), which indicates that it is a slender fox. Sexual dimorphism is small compared to other populations (Cavallini 1995). However, because we used foxes collected from October onwards, some not fully mature juveniles may have been included (sensu Travini and Delibes 1995). The growth curves of pup mass reach an asymptote in October-November (Lund 1959).

Acknowledgement

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Zusammenfassung

Der Rotfuchs in Norwegen: Morphologische Anpassung oder zufällige Größenvariation?

Daten zum Körpergewicht, zur Körper- und Schwanzlänge, sowie zur Kondition von 348 Rotfüchsen *Vulpes vulpes* aus drei verschiedenen Regionen (Süd-, Mittel- und Nord-)Norwegens wurden statistisch bearbeitet (Originaldaten: Lund 1959). Rüden wiesen in den Maßen, nicht aber in der Kondition signifikant höhere Werte auf als Fähen. Im Süden waren die Füchse kleiner als in Mittelnorwegen, am kleinsten und geschlechtsspezifisch am wenigsten dimorph waren sie im Norden des Landes. Bei den Rüden war die jährliche Variation größer. Im Herbst und Winter wiesen beide Geschlechter höhere Werte auf als im Sommer.

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Bevorzugt *Myotis emarginatus* kühlere Wochenstubenquartiere als *Myotis myotis*?

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Abstract

Does *Myotis emarginatus* prefer cooler nursery roosts than *Myotis myotis*?

In 1996 the roost sites chosen by a Bavarian nursery colony of *Myotis emarginatus* in relation to roost temperature was studied. The temperature preferences and the behaviour of *M. emarginatus* were compared with those of *Myotis myotis. M. myotis* and *M. emarginatus* generally avoid temperatures above 30 °C in their nurseries. Both species seem to tolerate or prefer higher temperatures at specific times or in specific circumstances. If available *M. emarginatus* will opt for roost sites with a temperature of at least 25 °C. *M. myotis* will start to cluster when temperatures fall below 20–25 °C to maintain a higher body temperature. No marked differences with respect to preferable temperatures at their roost sites were recorded in their nursery roosts. *M. myotis* and *M. emarginatus* react though in different ways to high temperatures: *M. myotis* commonly uses roost sites that become too hot on warm summer days. To counteract that the bats move apart in the course of the day (the cluster density decreases) and many individuals will move to cooler roost sites. *M. emarginatus* always forms close clusters (no distance between the individuals) and avoids roost sites in which temperatures are likely to become too high forcing the bats to move to another roost.

Key words: *Myotis emarginatus*, *M. myotis*, thermoregulation, reproduction, behaviour

Einleitung

Die Wimperfledermaus (*Myotis emarginatus*) gehört zu den Fledermausarten, die in Mitteleuropa zur Aufzucht der Jungen auf Gebäude (Dachböden) angewiesen sind. Wie auch das Große Mausohr (*Myotis myotis*) wählen Wimperfledermäuse meist offene Hangplätze im Quartier (z. B. an Dachbalken) und ziehen sich im Gegensatz zu vielen anderen Fledermausarten kaum in enge Verstecke zurück. Die von *M. emarginatus* bewohnten Dachstühle gelten im Vergleich zu Mausohrquartieren als kühl (Gaisler 1971; Issel und Issel 1953; Richarz et al. 1989). In einer oberbayerischen Kolonie stiegen die Temperaturen kaum über 30 °C (Richarz et al. 1989). In Mausohrwochenstuben werden regelmäßig 40 °C erreicht (Zahn 1995). Im deutlichen Gegensatz zu Mausohren nutzen Wimperfledermäuse kaum Hangplätze unmittelbar im First, dem wärmsten Bereich der Dachstühle.

Um zu untersuchen, ob Wimperfledermäuse tatsächlich niedrigere Temperaturen bevorzugen als Mausohren, wurden in der vorliegenden Arbeit die Temperaturen an den Hangplätzen einer Wimperfledermauswochenstube aufgezeichnet und die Hangplatzwahl bei unterschiedlichen Quartiertemperaturen verfolgt.

Material und Methode

Die untersuchte Kolonie im Dachstuhl des Schlosses Pertenstein (Landkreis Traunstein, Oberbayern) wurde aufgrund ihrer geringen Größe von nur 10 adulten Tieren gewählt, da individuenreichere Kolo-

nien empfindlicher auf Störungen reagieren als kleine Gruppen. Während erstere meist auffliegen, wenn man sich dem Hangplatz nähert (Richarz et al. 1989), zeigen letztere auch bei einem Beobachtungsabstand von nur einem Meter keine Reaktion. Der Dachboden des Schlosses weist eine Fläche von rund 180 m^2 auf und erreicht im First eine Höhe von 4 m. Das Ziegeldach ist innen mit Brettern verkleidet. An den Wänden zusammenlaufende Dachbalken bilden in verschiedenen Höhen geschützte, aber von unten offene und gut einsehbare Winkel, die von den Fledermäusen als Hangplätze genutzt werden. Anhand der Kotansammlungen aus dem Vorjahr wurden im April 1996 vor dem Erscheinen der Tiere 7 früher genutzte Hangplätze festgestellt.

Unter den beiden Hangplätzen mit den größten Kotmengen wurden im Abstand von jeweils 10 cm die beiden Meßfühler eines Fernthermographen angebracht, der die Temperatur durchgehend vom 15. 5. bis zum 21. 8. 1996 aufzeichnete. An den fünf weiteren Hangplätzen wurde in diesem Zeitraum bei wöchentlichen Kontrollen die Temperatur mit einem Meßfühler eines Handthermometers gemessen. Die Kontrollen erfolgten um 18.00 Uhr, da um diese Zeit das Temperaturmaximum im Dachstuhl erreicht wird. So konnten die Tageshöchsttemperaturen gemessen und verglichen werden. Bei jedem Besuch wurden aus einer Entfernung von etwa einem Meter die Hangplätze nach anwesenden Fledermäusen abgesucht. Adulte und Juvenile wurden anhand der Größe und der Fellfarbe unterschieden. Die Kotspuren unter den Winkeln wurden stets beseitigt, um festzustellen, welche Hangplätze in der vergangenen Woche aufgesucht worden waren. Hielten sich Fledermäuse bei einer Kontrolle an neuen, bisher nicht genutzten Hangplätzen auf, wurden die Temperaturen an diesen Stellen ebenfalls gemessen. Die Außentemperaturen wurden von der nächstliegenden Wetterstation (Marwang; Entfernung 13 km) zur Verfügung gestellt, die sich wie Pertenstein auf rund 530 m über N. N. befindet.

Ergebnisse

Die ersten sechs Wimperfledermäuse erschienen zwischen dem 2. und 9. 5. im Quartier. Am 10., 19. und 26. 6. wurden die meisten Adulten gezählt (Abb. 1). Am 26. 6. waren auch die ersten Jungtiere sichtbar. Am 4. 7. waren acht, ab dem 11. 7. noch fünf Junge vorhanden (als Prädatoren herabgefallener Jungtiere kamen Siebenschläfer in Frage). Ihre Zahl blieb wie die der Adulten bis zum 25. 7. konstant. Danach begann die Auflösung der Wochenstube, während der zwischen Adulten und Juvenilen nicht mehr unterschieden werden konnte. Die letzten zwei Individuen konnten am 21. 8. beobachtet werden.

Bis zum 26. 6. wurden die Tiere mit der Ausnahme vom 10. 6. in einer oder in zwei Gruppen aus 2 bis 7 Tieren angetroffen. Vom 4. bis zum 18. 7. ruhten alle Fledermäuse immer in einem Pulk. Die Tiere hielten dabei stets engen Körperkontakt. Erst ab dem 25. 7. hingen regelmäßig einige Koloniemitglieder einzeln an Hangplätzen, abseits der weiterhin stets Körperkontakt haltenden Gruppen aus 2 bis 11 Individuen.

Die Temperatur im Dachstuhl schwankte innerhalb eines Tages um maximal 18 °C

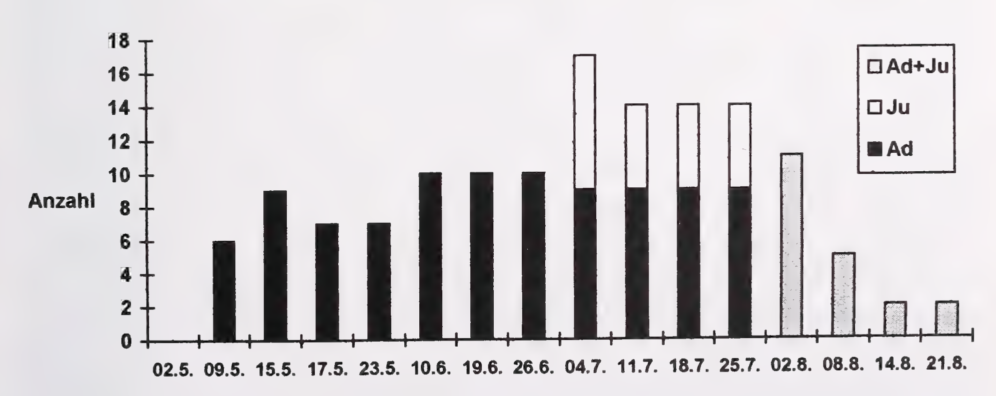


Abb. 1. Anzahl der an den Kontrollterminen (2. 5.–21. 8. 1996) im Quartier beobachteten Wimperfledermäuse (Ad = Adulte, Ju = Juvenile)

und damit etwas stärker als im Freien. Die durchschnittliche Tagesmitteltemperatur am wärmsten Hangplatz betrug in der zweiten Maihälfte 17 °C, im Juni 22 °C, im Juli 24 °C und vom 1. bis zum 21. August 22 °C. Die Tagesmitteltemperatur lag bis etwa 10 °C über den Tagesmittelwerten der Außentemperatur. Mit zunehmender Sonnenscheindauer im Lauf des Tages wurden die Unterschiede ausgeprägter. Am Morgen (5.30 Uhr) lag die Temperatur am wärmsten Hangplatz meist etwa 5–10 °C über der Außentemperatur, mittags (12.00 Uhr) wurden die Außenwerte um bis zu 10 °C und abends (20.00 Uhr) um bis zu 14 °C überschritten.

Bei Sonneneinstrahlung erwärmte sich der Dachstuhl im Bereich der oberen und zugleich wärmsten Hangplätze am Spätnachmittag regelmäßig auf über 30 °C (maximal 39 °C). Im Bereich der untersten Hangplätze lagen an diesen Tagen die maximalen Temperaturen um 4–6 °C darunter.

Insgesamt wurden von den Tieren 7 Hangplätze regelmäßig und 5 jeweils ein- bis zweimal genutzt. Alle Hangplätze befanden sich in den nach oben geschlossenen Winkeln zusammenlaufender Balken, direkt an den Wänden des Quartiers.

Vor der Geburt der Jungen hielten sich die Tiere an sechs verschiedenen Hangplätzen auf. Während die Wimperfledermäuse am 17. 5. einen Hangplatz im mittleren Temperaturbereich aufgesucht hatten (Abb. 2), nutzten sie am 23. 5., einem kalten Tag, den wärmsten zur Verfügung stehenden Platz. Gegen Ende der Tragzeit, am 10. 6. ruhten zwei Tiere an den beiden mit 39,3 °C bzw. 37,8 °C wärmsten Hangplätzen (die übrigen flogen bereits beim Betreten des Dachbodens umher), später wurden Temperaturen von über 30 °C jedoch gemieden.

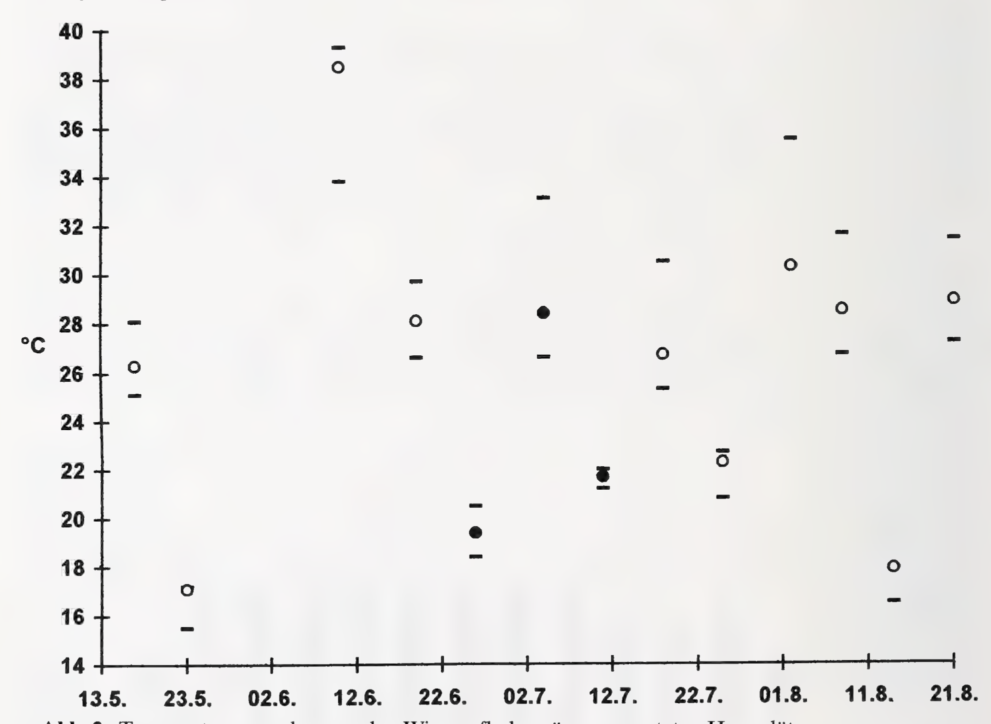


Abb. 2. Temperaturen an den von den Wimperfledermäusen genutzten Hangplätzen, gemessen um 18 Uhr; Kontrolltage: vgl. Abb. 1. Angegeben ist jeweils die Temperatur am wärmsten und am kältesten Hangplatz (–) sowie die Temperatur an dem bzw. den genutzten Hangplätzen (○, bzw. ● ab dem ersten Nachweis der Jungen bis zu deren Flugfähigwerden). Im Fall mehrerer an einem Kontrolltermin genutzter Hangplätze ist der Mittelwert der verschiedenen Temperaturen angegeben. Nutzten die Tiere den kältesten oder wärmsten Hangplatz, ist der untere bzw. obere Grenzwert (–) durch „○“ ersetzt.

Während der vermuteten Geburtsperiode (etwa 19.–26. 6.) und während der Zeit der Aufzucht der Jungen wurden die Fledermäuse immer an Hangplätzen im mittleren Bereich des zur Verfügung stehenden Temperaturspektrums angetroffen. Ab dem Zeitpunkt, an dem Jungtiere sichtbar waren (26. 6.), fanden bis zum 11. 7. keine Hangplatzwechsel statt: Die Tiere hielten sich immer im selben Balkenwinkel auf und Kot fehlte an anderen Stellen völlig. Dieser Hangplatz wies bei allen Kontrollen mittlere Temperaturen auf (Abb. 2). Der durchschnittliche Tagesmaximalwert betrug zwischen dem 19. 6. und dem 11. 7. nur 21 °C, am wärmsten Hangplatz hingegen 24 °C. Die höchste Tagesmaximaltemperatur betrug am Wochenstubenhangplatz in dieser Zeit 33 °C während am wärmsten Hangplatz 38 °C erreicht wurden.

Ab dem 18. 7. waren die Jungen flugfähig, und die Hangplätze wurden wieder regelmäßig gewechselt. Die Tiere verteilten sich mitunter auf mehrere Hangplätze (maximal 5, am 8. 8.) und auch Kotspuren waren wieder an verschiedenen Stellen zu finden. Insgesamt wurden nach dem 18. 7. noch 10 verschiedene Hangplätze genutzt.

Ab dem 25. 7. hielten sich Einzeltiere immer öfter an zuvor nicht genutzten Plätzen auf. An kalten Tagen (25. 7, 14. 8.) wurden die wärmsten, an einem heißen Tag (2. 8.) hingegen der kälteste zur Verfügung stehende Hangplatz genutzt. Da am 2. 8. Kot an allen anderen Hangplätzen fehlte, hatten die Tiere bereits an den ebenfalls warmen Tagen seit dem 25. 7. stets den kühlen Platz gewählt und nicht etwa während der kühleren Vormittagsstunden wärmere Balkenwinkel aufgesucht. Bei gemäßigten Temperaturen im Quartier (18. 7., 8. 8. und 21. 8.) wurden an den genutzten Hangplätzen Temperaturen zwischen 26 und 29 °C gemessen (Abb. 2).

Diskussion

Während der Gravidität und der Aufzucht der Jungen bildeten die Wimperfledermäuse stets dichte Pulks mit engem Körperkontakt. Dies konnte auch bei jährlichen Kontrollen in den übrigen bayerischen Wochenstuben beobachtet werden. Mausohren hingegen bilden dichte Gruppen bei Temperaturen unter 20–25 °C, wenn es sich lohnt, trotz niedriger Umgebungstemperatur eine hohe Körpertemperatur aufrechtzuerhalten, was durch einen engen Körperkontakt erleichtert wird (Audet 1992; Heidinger et al. 1989). In längeren Kälteperioden und bei hohen Temperaturen hängen Mausohren oft in lockeren Pulks oder einzeln. Bei einem Temperaturanstieg konnten Heidinger et al. (1989) ab einer Lufttemperatur am Hangplatz von 25 °C ein allmähliches Abwandern von stark erwärmten Brettern an benachbarte kühlere Balken beobachten, wobei die Tiere auch aus dem firstnahen Bereich herabrückten. Ab einer Lufttemperatur von etwa 30 °C flogen sie an kühlere Hangplätze. Zugleich verzichteten die Mausohren bei diesen Temperaturen weitgehend auf Körperkontakt, während die Wimperfledermäuse auch bei 30 °C noch einen engen Pulk bildeten. Auf Ortsveränderungen am Hangplatz, wie ein Herabrücken an den Balken, gab es bei *M. emarginatus* keine Hinweise. Auch Richarz et al. (1989) beobachteten Wechsel der am Morgen gewählten Hangplätze nur aufgrund von Störungen.

Die Nutzung unterschiedlicher Hangplätze an verschiedenen Tagen kann als Wahl eines je nach den herrschenden klimatischen Bedingungen passenden Platzes interpretiert werden. Hatten sie die Wahl, hielten sich Wimperfledemäuse an mindestens 25 °C warmen Hangplätzen auf. Richarz et al. (1989) berichten ebenfalls von häufigen Hangplatzwechseln vor der Geburt und nach dem Erwachsenwerden der Jungen. Ihre große Kolonie (ca. 90 Adulte) suchte nie geschützte Hangplätze wie die von den Pertensteiner Fledermäusen genutzten Balkenwinkel auf. Möglicherweise nutzen gerade kleine Kolonien solche Stellen, da sie trotz der Bildung dichter Pulks bei niedrigen Umgebungstemperaturen weniger Energie einsparen als größere Gruppen (Audet 1992; Tuttle 1975). Die nach oben abgeschlossenen Winkel bieten einen energetischen Vorteil, da der Aus-

tausch der von den Tieren erwärmten Luft verringert wird. Während der Gravidität halten Mausohren und auch andere Fledermausarten eine hohe Körpertemperatur (30–37 °C) selbst bei niedriger Umgebungstemperatur aufrecht, so daß die Embryonalentwicklung nicht verzögert wird (Audet und Fenton 1988; Audet 1992; Heidinger et al. 1989; Speakman und Racey 1987). Die Wimperfledermäuse könnten sich aus diesem Grund während der späten Gravidität (23. 5. und 10. 6.) an den wärmsten Hangplätzen aufgehalten haben, da es für sie hier am einfachsten war, die Körpertemperatur hoch zu halten. Während der Jungenaufzucht suchten die Tiere Hangplatzwechsel offensichtlich zu vermeiden, da sie sich stationär an einem durchschnittlich warmen Platz aufhielten, an dem bei Hitze keine zu starke Erwärmung zu erwarten war. Mausohren nutzen während der Aufzucht meist Hangplätze, die sich schnell und stark erwärmen, fliegen jedoch an zu heißen Tagen an kühlere Alternativplätze, wobei kleinere Junge mitgenommen werden, während ältere Junge kletternd erträgliche Temperaturbereiche aufsuchen (Bilo 1990; Heidinger et al. 1989). Bei kühlem Wetter während der Jungenaufzucht fällt *M. myotis* meist in Tageslethargie (Heidinger et al. 1989; Audet 1992). Ob sich *M. emarginatus* ähnlich verhält, konnte aufgrund der fehlenden Körpertemperaturmessungen nicht festgestellt werden.

Nachdem die Jungen flugfähig geworden waren, schienen die Wimperfledermäuse – soweit verfügbar – Hangplatztemperaturen zwischen 26 und 29 °C zu bevorzugen. Es ist anzunehmen daß bei diesen Temperaturen und bei engem Körperkontakt leicht Körpertemperaturen aufrecht erhalten werden können, die den Tieren volle Aktivität gestatten. Mausohren nutzen in dieser Zeit wieder meist die soziale Thermoregulation, versuchen also durch Gruppenbildung eine hohe Körpertemperatur aufrecht zu erhalten (Heidinger pers. comm.).

Obwohl *M. myotis* und *M. emarginatus* im Wochenstubenquartier Lufttemperaturen am Hangplatz von über 30 °C in der Regel meiden, gibt es für beide Arten Hinweise auf eine Bevorzugung bzw. Tolerierung höherer Temperaturen zu bestimmten Zeiten oder unter bestimmten Umständen: während der späten Gravidität ruhten zwei Koloniemitglieder an den mit 39,3 °C bzw. 37,8 °C wärmsten Hangplätzen und während der Jungenaufzucht wurden am stationär genutzten Hangplatz im Lauf von 20 Tagen zweimal Temperaturen von über 30 °C erreicht (31 und 33 °C). Manche Mausohren bevorzugten bei den Temperaturwahlversuchen von Röszner (1953) Umgebungstemperaturen von über 30 °C.

Nach den Ergebnissen bisheriger Untersuchungen zeigen beide Arten somit keinen deutlichen Unterschied hinsichtlich der Vorzugstemperatur an den Hangplätzen in den Wochenstuben.

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Zusammenfassung

In einer oberbayerischen Wochenstube der Wimperfledermaus (*Myotis emarginatus*) wurde im Sommer 1996 die Hangplatzwahl in Abhängigkeit von der Umgebungstemperatur untersucht und mit den bekannten Verhaltensweisen und Ansprüchen des Großen Mausohrs (*Myotis myotis*) verglichen. Sowohl *M. myotis* als auch *M. emarginatus* meiden im Wochenstubenquartier in der Regel Lufttemperaturen am Hangplatz von über 30 °C. Bei beiden Arten gibt es Hinweise auf eine Bevorzugung bzw. Tolerie-

rung höherer Temperaturen zu bestimmten Zeiten oder unter bestimmten Umständen. Haben sie die Wahl, halten sich Wimperfledermäuse an mindestens 25 °C warmen Hangplätzen auf. Sinken an Mausohrhangplätzen die Temperaturen unter 20–25 °C, beginnen die Tiere die soziale Thermoregulation einzusetzen, so daß sie nicht in Lethargie fallen sondern eine hohe Körpertemperatur aufrecht erhalten. Hinweise auf deutliche Unterschiede hinsichtlich der Vorzugstemperatur an den Hangplätzen in den Wochenstubenquartieren ergaben sich nicht. Doch weichen Mausohren und Wimperfledermäuse zu hohen Temperaturen auf unterschiedliche Weise aus: Während *M. myotis* sich schnell erwärmende Hangplätze wählt, aber bei zu starker Erwärmung die Individuendichte verringert und unter Umständen den Hangplatz wechselt, bildet *M. emarginatus* stets dichte Gruppen und meidet von vornherein Hangplätze, an denen eine zu starke Erwärmung wahrscheinlich ist.

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Cytogenetics of *Graomys griseoflavus* (Rodentia: Sigmodontinae) in central Argentina

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Abstract

The distribution of karyomorphs of the *Graomys griseoflavus* species complex (2 n = 42 and 2 n = 36–38) is described for six localities from central Argentina, providing additional information for Córdoba, La Pampa and La Rioja provinces. Comments regarding the biogeography and systematics of this species complex are provided.

Key words: *Graomys griseoflavus*, Rodentia, karyology, distribution, central Argentina

Introduction

Graomys griseoflavus, commonly known as pericote común or pericote de vientre blanco, has been reported to possess widely variable diploid chromosome numbers of 34, 35, 36, 37, 38, 41, and 42 (Wainberg and Fronza 1974; Pearson and Patton 1976; Theiler and Gardenal 1994; Zambelli et al. 1994; Theiler and Blanco 1996 a, b). Despite being a widespread species (Hershkovitz 1962), no data are available on the cytogenetics of this species in La Pampa Province. Additionally, the extent of chromosomal variation remains to be assessed in vast portions of the distribution of the species.

According to Siegenthaler et al. (1990 a, b) *Graomys griseoflavus* is widespread in the La Pampa Province. It occurs in habitats generally associated with wooded or shrubbed areas, in almost all the western part of the Province, being absent in the eastern Pampean grasslands portion. *Graomys griseoflavus* has been collected along roadside rights-of-ways associated with woody cover, rock outcroppings and in human dwellings. In Mendoza Province, the species occupies a variety of habitats including orchards, badlands, Monte Desert and Precordillera up to an altitude of 1950 m (Rosi 1983).

The focus of this study is to further document the extent of chromosomal variation in *Graomys griseoflavus*, providing additional information for Córdoba, La Pampa and La Rioja provinces.

Material and methods

A total of 19 *Graomys griseoflavus* specimens were live-trapped using a variety of Sherman, Davis, and wire mesh traps. The standard procedure of in vivo colchicine mitotic arrest was used for obtaining chromosomes from bone marrow. In most cases, the yeast stress method (Lee and Elder 1980) was used to obtain an increased mitotic index. Slides were prepared by dropping the cell suspension from a 50–60 cm height into a large drop of distilled water on the surface of the slide (Baker et al. 1982). Chromosome slides were observed and photographed and the diploid number and chromosomal morphology

was determined for each specimen. All voucher specimens were prepared as standard study skins and skulls and are housed in the collections of Texas Tech University Museum (TTU), TK numbers identify slides and cell suspensions referenced to voucher specimens; of La Pampa Vertebrate Survey (RVP, Plan de Relevamiento de los Vertebrados de la Provincia de La Pampa), deposited in the Museo Provincial de Historia Natural, Santa Rosa, La Pampa; and in the Colección Mastozoológica Orientación Anatomía Comparada of the Universidad Nacional de Rio Cuarto (UNRC), Rio Cuarto, Córdoba, Argentina.

Localities sampled and specimens examined:

La Rioja Province: 1. General San Martin Department, Ulapes, 2 km N (n = 2), one male (TK 49047), one female (TK 49048).

Córdoba Province: 2. Cruz del Eje Department, Palo Parado, 30 km NW Cruz del Eje (n = 2), two females (TK 40655–40656).

La Pampa Province: 3. Toay Department, 10 km SW Santa Rosa, Chacra La Lomita (n = 8), three males (TK 49171–49173), five females (TK 49169–49170, 49174–49175, 49177). 4. 12 km NNE Naicó, Estancia Los Toros (n = 3), two females (TK 27891–27892), one male (TK 27893). 5. Puelén Department, 25 km SE Puelén, NE border of Salitral de La Perra, Puesto Rogueira (n = 1), one male (TK 47611). 6. Caleu Caleu Department, 40 km N Anzoategui, Almacén El 52 (n = 3), three females (TK 27894–27895, 40634).

Results and discussion

The four specimens from La Rioja and Córdoba provinces possessed a 2 n = 42 karyotype consisting of a pair of large submetacentric chromosomes, two smaller pairs of submetacentrics and the remainder of the autosomes being acrocentrics grading in size from large to small. The X chromosome is a medium sized submetacentric and the Y an acrocentric chromosome. This karyotype has been previously recorded for localities in La Rioja, Córdoba and Catamarca provinces (Theiler and Gardenal 1994; Zambelli et al. 1994). From La Pampa Province, the karyotypic data show the pattern that includes 36, 37, and 38 chromosome diploid numbers. The 2 n = 36 karyotype consists of a pair of large metacentrics, four pairs of medium sized and small submetacentrics and the rest of the autosomes are acrocentric (Fig. 1). In the case of the 2 n = 37 variant, the first pair of autosomes is heteromorphic consisting of a large metacentric and two small acrocentrics as its homologues (Zambelli et al. 1994). In the case of the 2 n = 38 there exist two extra pairs of acrocentrics instead of the large metacentric pair as in the 2 n = 36 form. The pre-

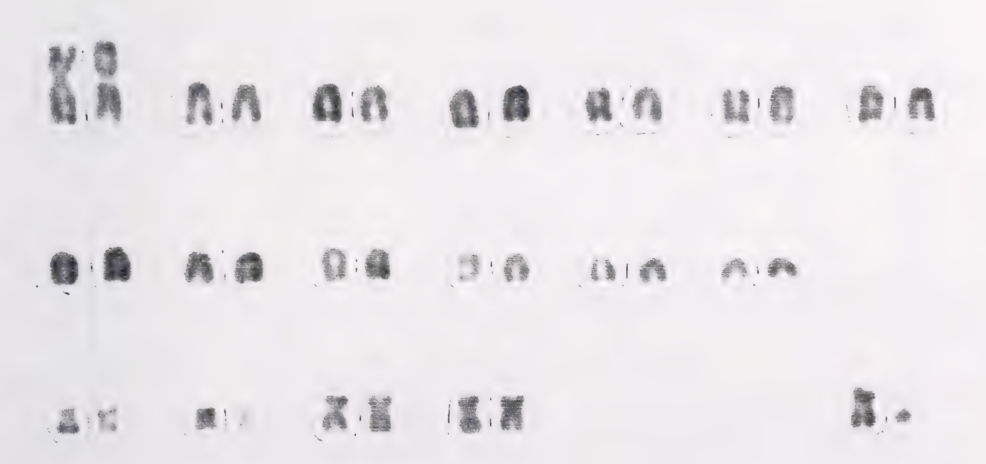


Fig. 1. 2 n = 36 *Graomys griseoflavus* karyotype (TK 47611, male) from Salitral de La Perra, 25 km SE Puelén, La Pampa.

sent distributional data are in concordance with data for the neighboring Buenos Aires Province (Chasicó, Medanos), and the central-western area of Argentina, which include portions of Mendoza and Catamarca provinces (Theiler and Gardenal 1994; Theiler and Blanco 1996a, b). The 2n = 36–38 and 2n = 42 forms are interrelated through a number of chromosomal rearrangements that include pericentric inversions and Robertsonian fusions (Zambelli et al. 1994). Interbreeding between these forms under laboratory conditions only occurs between 2n = 36–38 females and 2n = 42 males. The hybrids, are sterile (100% of males) or have diminished fertility (23% of females), and have 2n = 39 or 40 (Theiler and Gardenal 1994; Theiler and Blanco 1996b). Individual females in estrus are capable of recognizing odors of compatible homomorphic mating partners. Avoidance of heteromorphic mating partners by these females, allows for premating isolation to occur (Theiler and Blanco 1996b). Protein electrophoresis studies comparing both sets of cytotypes showed genetic identity values (0.911 and 0.915) that would correspond to the same species (Theiler and Gardenal 1994).

Regarding the geographic distribution (Fig. 2), the 2n = 36, 37, and 38 forms have been attributed to the Monte Desert, and the 2n = 42 forms to the Espinal, with both forms overlapping in transition areas (Theiler and Blanco 1996a, b). In this report, the 2n = 36, 37, and 38 karyotypes were found at localities belonging to the Caldén (*Prosopis caldenia*) District of the Espinal (Los Toros, Almacén El 52 and La Lomita), and at one locality belonging to the Monte Desert (Puelén) (Cabrera 1976). Thus, in a biogeographic interpretation, the 2n = 42 complex seems to have more defined Chacoan affinities. In the case of the 36–38 complex, it would appear to be restricted to the Monte Desert and the southern portion of the Espinal. Nevertheless, limits between these biogeographical areas are not precise, generally forming vast ecotones and mosaics (Cabrera 1976). The Espinal is considered as an impoverished Chaco, and allows for the southward expansion of several species representative of the Chacoan fauna.

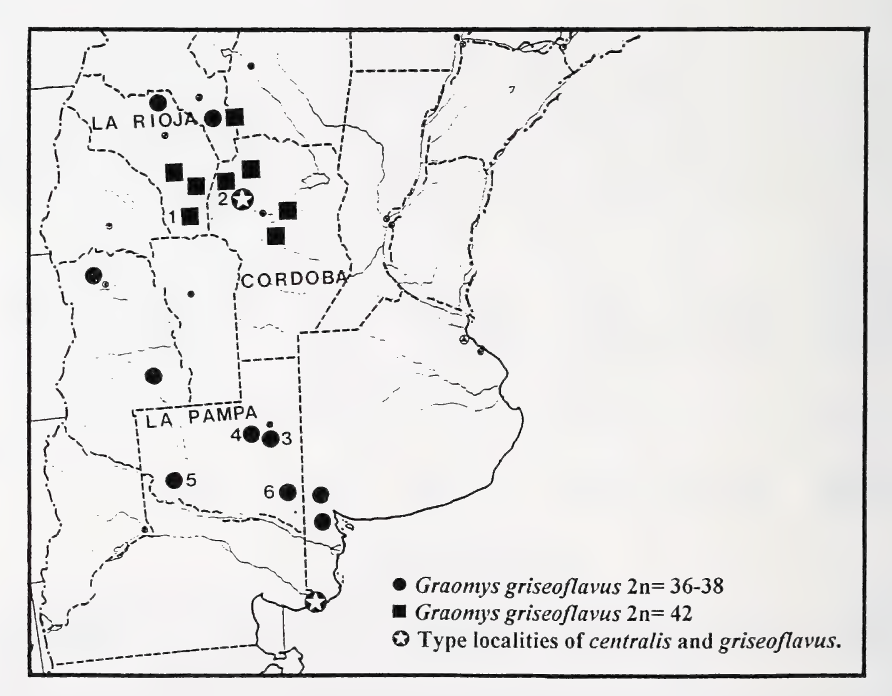


Fig. 2. Map of central Argentina showing the distribution of karyomorphs of *Graomys griseoflavus* (pooled from the literature and this report).

Despite the growing evidence that the 42 and 36–38 forms represent different species (Theiler and Blanco 1996 a), the nomenclatorial situation that is involved has not been addressed. In the particular case of available names for these taxa in central Argentina, it would be possible to assign the 2 n = 42 forms to *centralis*, type locality Cruz del Eje, Córdoba Province, described as a subspecies of *griseoflavus* (under the genus *Eligmodontia*) by Thomas (1902). The present locality of Palo Parado (30 km NW of Cruz del Eje) is the nearest with a documented 2 n = 42 specimen of *Graomys*. For the 2 n = 36–38 forms the name *griseoflavus* Waterhouse, 1837 (type locality, Rio Negro) could be applied. Nevertheless, before invoking these changes, the status of other named putative taxa inhabiting central Argentina, such as *edithae* Thomas, 1919 (Otro Cerro, NE La Rioja), and *medius* Thomas, 1919 (Chumbicha, Catamarca) should be assessed. The taxon *edithae* has been considered valid by Redford and Eisenberg (1992); valid, but of uncertain status by Musser and Carleton (1993); and also valid, but considering that it could be "a high-elevation smaller-bodied offshoot of *G. griseoflavus" by* Braun (1993). The taxon *medius* is generally referred to as a synonym of *griseoflavus* (Musser and Carleton 1993). Additionally, other species of *Graomys* for which there is available cytogenetical information is *domorum*, with a 2 n = 28 (Pearson and Patton 1976). The resolution of these problems coupled with the assessment of the geographic distribution of *Graomys* karyomorphs should include cytogenetics in the type localities. This information will shed more light on the systematic status of this species complex.

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Zusammenfassung

Zytogenetik von Graomys griseoflavus (Rodentia: Sigmodontinae) in Mittelargentinien

Die Verteilung der Karyomorphen des *Graomys griseoflavus*-Artkomplexes (2 n = 42 und 2 n = 36–38) wird für sechs Gebiete aus Mittelargentinien beschrieben. Damit liegen neue Daten für die Provinzen Córdoba, La Pampa und La Rioja vor. Die Ergebnisse werden im Zusammenhang mit der Biogeographie und der Systematik des Artkomplexes diskutiert.

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Systematics and distribution of *Mastomys* (Muridae, Rodentia) from Ethiopia, with the description of a new species

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Abstract

Studied was morphological, allozymic, and chromosomal variation of Ethiopian *Mastomys natalensis* sensu lato to clarify the systematics of this species complex. Three different species of *Mastomys* occur in Ethiopia. A new species, *Mastomys awashensis* n. sp., is described and compared with the other two, *M. erythroleucus* and *M. natalensis* which are widely distributed throughout most of Western, Central, and Eastern Africa. *Mastomys awashensis* n. sp. is endemic to the Ethiopian Rift Valley and is known only from two localities in the Upper Awash Valley. This newly described species differs from the other two Ethiopian *Mastomys* species by fixed alleles at Ldh-B and Got-1 loci and also by Hbb patterns and by relatively shorter tail bearing smaller scales. Besides that, the three species co-existing in the middle part of the Ethiopian Rift Valley can be distinguished biometrically with the use of multivariate analysis. The karyotype of *M. awashensis* (2 n = 32, NFa = 54) which is similar to that of *M. natalensis*, demonstrates, nevertheless, a number of unique characteristics differing it from any known representative of the *M. natalensis* species complex. The presented results from different disciplines support a previous supposition of a "mosaic" evolution under divergence in this species group.

Key word: *Mastomys*, Ethiopia, craniometry, allozymes, chromosomes

Introduction

The multimammate rat, genus *Mastomys* Thomas, 1915, is widely distributed throughout sub-Saharan Africa. It includes up to eight species (for review, see Musser and Carleton 1993). They are distinguished mainly by chromosomal and biochemical traits, so the data on their relations and peripheral distribution remain largely uncertain. Of these, four most closely related and weakly separable species *M. coucha* (Smith, 1836), *M. erythroleucus* (Temminck, 1853), *M. hildebrandtii* (Peters, 1878), and *M. natalensis* (Smith, 1834) constitute a presumably monophyletic group called the *M. natalensis* species complex that occupies most of the genus distribution region.

The situation with *Mastomys* taxonomy in Ethiopia is a matter of controversy, as well. All Ethiopian *Mastomys* were lumped under *M. natalensis* (Yalden et al. 1976). At present, two species are commonly acknowledged in Eastern and Central Africa, *M. erythroleucus* (2 n = 38) and *Mastomys* with 2 n = 32, NFa = 54 (Hubert et al. 1983). It has been supposed once that multimammate rats with latter karyotype belong to two separate species, *M. huberti* (Wroughton, 1908) and *M. natalensis* sensu stricto, inhabiting Western to Eastern and Southern Africa, respectively (Robbins and van der Straeten 1989; Leirs et al. 1991). Recently, the conspecificity of these two taxa was shown by cytogenetic, biometric, and hybridological analyses (Britton-Davidian et al. 1995; Granjon et al. 1996).

The present study provides allozymic, cytogenetic, and morphological information on the Ethiopian *Mastomys* sibling-species. *Mastomys* specimens collected in Ethiopia during 1987–1993 appeared to belong to three different species. Two of them corresponded to widespread species: *M. natalensis* (2 n = 32, NFa = 54) and *M. erythroleucus* (2 n = 38, NFa = 50). The other one (2 n = 32, NFa = 54, specific Hbb pattern) was shown to represent a separate species which is described here.

Material and methods

Field work in Ethiopia was carried out in the framework of the Joint Ethio-Russian Biological Expedition (JERBE). Specimens were captured at the following localities: 1. Awash National Park: 09°00′ N 40°10′ E; 2. Koka Lake area: 08°23′ N 39°09′ E; 3. Ambo area: 08°56′ N 37°58′ E; 4. Gambela area: 07°53′ N 34°22′E; 5. Lower Omo Valley: 05°00′ N 36°07′ E; 6. Nechisar National Park: 05°53′ N 37°38′ E. All specimens referred to in the present publication are stored at the Zoological Museum of Moscow University (ZMMU) and the Natural History Museum, Addis Ababa (NHMAA).

Allozymic study: According to allozyme characters the whole sample of Ethiopian *Mastomys* was divided into three groups corresponding presumably to three species: *M. erythroleucus* (locality 2: N = 27); *M. natalensis* (2: N = 6, 3: N = 79); *Mastomys* n. sp. (1: N = 4, 2: N = 7). Standard vertical polyacrylamide and horizontal starch gel electrophoresis and standard protein staining techniques (Davis 1964; Peacock et al. 1965; Selander et al. 1971; Harris and Hopkinson 1978) were used to assay 20 enzymatic and non-enzymatic proteins from blood and kidney tissues. The enzymatic proteins (their respective abbreviations and tissue used are given in parentheses) were adenylate kinase (Ak, kidney); creatine kinase (Ck, kidney); glucosephosphate isomerase (Gpi, kidney); glycerol-3-phosphate dehydrogenase (Gpd, kidney); glutamate-oxaloacetate transaminase (Got-1, Got-2, kidney); isocitrate dehydrogenase (Idh-1, Idh-2, kidney); lactate dehydrogenase (Ldh-A, Ldh-B, kidney); malate dehydrogenase (Mdh-1, Mdh-2, kidney); malic enzyme (Me-1, blood); phosphoglucomutase (Pgm, kidney); purine nucleoside phosphorylase (Np, blood); phosphogluconate dehydrogenase (Pgd, blood); sorbitol dehydrogenase (Sdh, kidney); superoxide dismutase (Sod-1, Sod-2, kidney). The non-enzymatic protein was haemoglobin (Hbb). The specimens from localities 4 (*M. erythroleucus*: N = 48, *M. natalensis*: N = 15) and 6 (*M. erythroleucus*: N = 12) were analyzed only as to their haemoglobin patterns. Genetic relationships between *Mastomys* species were investigated using *Praomys albipes* (Ruppell, 1842) (localities 7 [Addis Ababa]: N = 26, 3: N = 26) and *Praomys fumatus* (Peters, 1878) (locality 2: N = 2) as the representatives of the closest related genus for comparison.

Cytogenetic study: The chromosomal analysis was performed on *M. erythroleucus* from localities 2 (10 males, 5 females), 5 (1 male), 6 (5 males, 3 females); *M. natalensis* from 2 (1 male, 3 females), 3 (3 males, 1 female), and *Mastomys* n. sp. from 1 (3 males, 1 female), 2 (5 males, 4 females). Somatic metaphases were prepared from bone marrow by the usual air-drying technique according to Ford and Hamerton (1956) or through short-termed tissue culture from dead animals (Kozlovsky 1974). Slides were stained with 4% Giemsa in phosphate buffer with pH = 7.0. C-banding was obtained according to Sumner (1972).

Morphological study: Four standard external measurements were obtained from freshly killed rats: head-body length (L), tail length (C), hind foot length without claws (Pl), ear length (Au). The following standard skull characters were measured: condylobasal length (Cb), length of nasals (LoNos), length of frontals (LoFr), length of parietals (LoPar), length of anterior palatal foramen (LoFIn), length of diastema (LoDia), length of maxillary toothrow (LoM^{1-3}), greatest breadth of nasals (LaNos), zygomatic breadth (LaZig), width of ramus superior of processus zygomaticus ossis maxillaris (Lars), width of the zygomatic arch (Laaz), interorbital breadth (LaIor), length of mandibula (LoMd), length of mandibular toothrow (LoM_{1-3}), length of the third lower molar (LoM_3). All external and three cranial measurements (Cb, LaZig, LoMd) were recorded using a digimatic calliper, the other were taken by micrometer in binocular microscope MBS-9 (Russia). Based upon the degree of tooth wear, the specimens were grouped into three age classes: sub-adults, adults, and seniles. Only adult individuals were used for subsequent analyses.

Numerical analyses: Genetic distances among populations and species were calculated using BIOSYS programme (Swofford and Selander 1981). Statistic significance of differences among sexes and species by morphometric traits was evaluated by Student's t-test. Principal component analyses

were performed on external and cranial measurements of adult *Mastomys* specimens from the Ethiopian Rift Valley (localities 1, 2, and 6) using the subprogramme FACTOR of SPSS programme package (Nie et al. 1975) to evaluate unevenness of distribution of the specimens in the phenetic hyperspace of morphometric characters.

Results

Allozymic data

Only three of the 20 loci analyzed (Got-2, Mdh-2, and Sod-2) were found to be monomorphic for the same allele in *Praomys* and *Mastomys* species. The allele frequencies of both polymorphic and discriminant loci in the populations analyzed are given in table 1. Eight loci (Ak, Ck, Gpi, Idh-2, Ldh-A, Mdh-1, Pgd, and Hbb) discriminate the genera *Mastomys* and *Praomys*, five loci (Got-1, Ldh-B, Np, Pgd, and Hbb) discriminated at least two of the three *Mastomys* species. *Mastomys* n. sp. and *M. natalensis* from the middle part of the Ethiopian Rift Valley differ mutually by alternative alleles flxed for all these loci. The lack of heterozygous individuals at five diagnostic loci suggests the species rank of these sympatric taxa with similar karyotypes (2 n = 32). One locus (Hbb) appeared to be diagnostic for each of the three Ethiopian *Mastomys* species.

Table 1. Allele frequencies at 16 loci and frequencies of electrophoretically detectable phenotypes at Hbb licus in 8 populations belonging to 5 species of *Mastomys* and *Praomys* genera

	Species / Locality							
	Mastomys natalensis		*M. awashensis*		*M. erythroleucus*	*Praomys albipes*		*P. fumatus*
Locus, allele	3	2	2	1	2	3	7	2
Ak								
N	6	2	7	4	25	10	10	2
100	1.000	1.000	1.000	1.000	1.000	–	–	–
80	–	–	–	–	–	1.000	1.000	1.000
Ck								
N	79	5	7	4	27	26	29	2
156	–	–	–	–	–	1.000	1.000	1.000
100	1.000	–	1.000	1.000	1.000	–	–	–
56	–	1.000	–	–	–	–	–	–
Got-1								
N	79	6	7	4	27	26	29	2
138	–	–	–	–	0.019	–	–	–
100	0.987	1.000	–	–	0.981	–	–	–
87	–	–	1.000	1.000	–	0.962	1.000	1.000
67	0.013	–	–	–	–	0.038	–	–
Gpd								
N	79	5	7	4	26	26	29	2
145	–	–	–	–	–	0.077	–	–
135	–	–	–	–	–	0.058	–	–
113	–	–	–	–	0.962	–	–	–
100	1.000	0.900	–	–	0.038	0.846	1.000	1.000
67	–	0.100	1.000	1.000	–	–	–	–
44	–	–	–	–	–	0.019	–	–

Table 1. (continued)

	Species / Locality							
	Mastomys natalensis		*M. awashensis*		*M. erythroleucus*	*Praomys albipes*		*P. fumatus*
Locus, allele	3	2	2	1	2	3	7	2
Gpi								
N	79	5	7	4	27	26	29	2
112	–	–	–	–	–	–	0.190	–
58	–	–	–	–	–	1.000	0.810	1.000
–23	1.000	1.000	1.000	1.000	1.000	–	–	–
Idh-1								
N	79	6	7	4	26	26	29	2
100	–	–	–	–	–	0.077	0.224	–
78	0.814	1.000	0.714	1.000	0.923	0.712	0.466	1.000
64	0.186	–	0.286	–	0.077	0.212	0.310	–
Idh-2								
N	79	4	6	4	23	26	29	2
–50	1.000	1.000	1.000	1.000	1.000	–	–	–
–100	–	–	–	–	–	1.000	1.000	1.000
Ldh-A								
N	79	6	7	4	27	26	29	2
100	–	–	–	–	–	1.000	1.000	–
70	1.000	1.000	1.000	1.000	1.000	–	–	–
40	–	–	–	–	–	–	–	1.000
Ldh-B								
N	79	6	7	4	27	26	29	2
108	–	–	1.000	1.000	–	0.038	0.070	–
100	0.987	1.000	–	–	1.000	0.962	0.830	1.000
86	0.013	–	–	–	–	–	0.100	–
Me-1								
N	79	6	7	4	27	26	29	2
89	–	–	–	–	–	1.000	1.000	–
81	0.057	–	–	–	–	–	–	–
62	0.943	1.000	1.000	1.000	1.000	–	–	1.000
Mdh-1								
N	79	5	7	4	27	26	29	2
95	–	–	–	–	–	1.000	1.000	1.000
88	1.000	1.000	1.000	1.000	1.000	–	–	–
Np								
N	3	6	7	3	26	2	21	2
113	1.000	1.000	–	–	–	1.000	0.900	–
105	–	–	–	–	–	–	–	0.250
100	–	–	1.000	1.000	1.000	–	0.100	–
94	–	–	–	–	–	–	–	0.750
Pgd								
N	79	6	7	4	27	26	29	2
120	–	–	–	–	–	–	–	1.000
100	–	–	1.000	1.000	1.000	–	–	–
95	1.000	1.000	–	–	–	–	–	–
90	–	–	–	–	–	1.000	1.000	–

Table 1. (continued)

	Species / Locality							
	Mastomys natalensis		*M. awashensis*		*M. ery-throleucus*	*Praomys albipes*		*P. fumatus*
Locus, allele	3	2	2	1	2	3	7	2
Pgm								
N	79	6	7	4	26	26	29	2
110	0.006	0.333	–	–	–	–	–	–
100	0.981	0.667	1.000	1.000	1.000	1.000	1.000	1.000
87	0.013	–	–	–	–	–	–	–
Sdh								
N	79	5	7	4	25	26	29	2
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	–
80	–	–	–	–	–	–	–	1.000
Sod-1								
N	79	6	7	4	27	26	29	2
100	1.000	1.000	1.000	1.000	1.000	–	–	1.000
72	–	–	–	–	–	0.308	–	–
56	–	–	–	–	–	0.692	1.000	–
Hbb								
N	79	6	7	2	22	26	29	2
100/60 (1)	1.000	1.000	–	–	–	–	–	–
70/85	–	–	–	–	–	1.000	1.000	–
80/100 (4)	–	–	1.000	1.000	–	–	–	–
70/80	–	–	–	–	–	–	–	1.000
80/115 (2)	–	–	–	–	1.000	–	–	–

N – number of specimens examined. See text numbers of sampling localities. In parenthesis Hbb phenotypes are given according to LAVRENCHENKO et al. (1992).

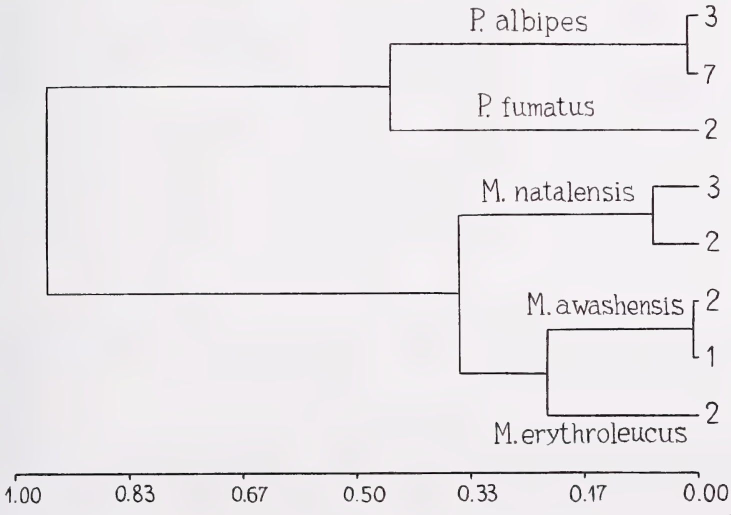


Fig. 1. UPGMA phenogram based on Nei's genetic distances between Ethiopian populations of *Mastomys* and *Praomys* species. The scale to be values of genetic distances (NEI 1972). See text for numbers of localities.

UPGMA dendrogram (Fig. 1) generated on the Nei's genetic distances matrix (Nei 1972) clearly shows that all *Mastomys* species are more closely related to each other than to Praomys. These results confirm the validity of the genus *Mastomys* as a monophyletic group.

The value of Nei's genetic distance between *M. erythroleucus* and *M. natalensis* is 0.258. *Mastomys* n. sp. genetically is more similar to *M. erythroleucus* (Dnei = 0.225) and is more distant from *M. natalensis* (Dnei = 0.402).

The scale of genetic distances between the three Ethiopian *Mastomys* is equal to that found between *Mastomys* species from Senegal (Duplantier et al. 1990 b). Ethiopian *Mastomys* n. sp. shares common fixed haemoglobin electromorph (Hbb 4) with *M. coucha* from South Africa (Gordon 1978; Green et al. 1978, 1980; Gordon and Watson 1986) and differs from the Ethiopian populations of *M. erythroleucus* (Hbb 2, 3) and *M. natalensis* (Hbb 1) (Lavrenchenko et al. 1992).

Chromosomal data

Ethiopian *M. erythroleucus* is characterized by 2 n = 38 which generally corresponds to results from previous studies of this species from other regions (Matthey 1965, 1966; Kral 1971; Tranier 1974; Hubert et al. 1983; Duplantier et al. 1990 a; Britton-Davidian et al. 1995). Therefore, we consider here the data on the two *Mastomys* species with a karyotype of 2 n = 32 only.

In *M. natalensis* (Fig. 2 a), the karyotype comprises 7 pairs of large submetacentric, 5 pairs of medium sized meta-submetacentric, and 3 small acrocentric pairs of autosomes. The smallest pair of autosomes has very short arms and sometimes it can be described as a subtelocentric. The sex chromosomes are both large, X being metacentric and Y being acrocentric. C-banding (Fig. 2 b) reveals all chromosome pairs carrying pericentromeric heterochromatin, and the short arms of chromosomes Nos. 1, 3, 4, 6 and 7 are extremely heterochromatic. The intercalaric heterochromatin of autosomes is indistinguishable. The X-chromosome is weakly stained, intensity of its staining is increased in centromeric and telomeric regions. The Y-chromosome appears fully heterochromatic.

In *Mastomys* n. sp., the chromosomal set (Fig. 3 a) includes 12 pairs of biarmed and 3 pairs of acrocentric autosomes. Biarmed autosomes contain a series of gradually decreasing in size (from large to medium sized) meta-submetacentric elements (10 pairs) and 2 pairs of small meta-subtelocentric autosomes. The most part of large biarmed autosomes belong to metacentric elements. The X-chromosome is one of the largest meta-submetacentrics, the Y-chromosome is a small submetacentric element. C-banding of karyotype (Fig. 3 b) reveals pericentromeric heterochromatin in all autosomes. Most of the autosomes have strong pericentromeric heterochromatic blocks, three biarmed pairs have weakly stained centromeric regions. Besides pericentromeric heterochromatin in two pairs of biarmed autosomes, the blocks of intercalaric heterochromatin of proximal (on the long arm of the 1st pair) and medial (on the short arm of the 5th pair) localization were also marked. The heterochromatin of short arms of autosomes was not revealed. The X-chromosome is not uniform: one of its arms is stained more intensively in the pericentromeric and telomeric regions, and there is a large distinct C-band located distally in the other arm. The Y-chromosome is fully heterochromatinized. This chromosome is stained more intensively in its pericentromeric part.

Comparison of karyotypes of *Mastomys* n. sp. and *M. natalensis* shows that they are distinguished from each other by: 1) the prevalence of metacentric elements in the group of large autosomes in former, while in *M. natalensis* this group is represented by mainly submetacentric elements; 2) the form of the Y-chromosome which is small submetacentric in *Mastomys* n. sp. and large acrocentric in *M. natalensis*; 3) the C-banding pattern which shows absence of heterochromatin of additional short arms in *Mastomys* n. sp.



Fig. 2. Karyograms of *Mastomys natalensis*: a: conventional staining by Giemsa; b: C-banding.

Morphometric data

Univariate procedures used to test differences between sexes did not reveal any effect of sexual dimorphism in our data. We therefore carried out all further analyses by combining both sexes.

According to the first step of PCA applied to three *Mastomys* species from the Ethiopian Rift Valley (Awash National Park, Koka Lake area, and Nechisar National Park), the first, second, and third components contain 43.1%, 11.3%, and 9.4% of the total variation, respectively. On the scatter plot of the first and third axes of the PCA (Fig. 4), *M. natalensis* is clearly separated from the remaining taxa. As to the latter, the specimens identified as *Mastomys* n. sp. and *M. erythroleucus* form one solid group.



Fig. 3. Karyograms of *Mastomys awashensis* n. sp.: a: conventional staining by Giemsa; b: C-banding.

A second PCA was elaborated to examine discrimination between *Mastomys* n. sp. and *M. erythroleucus*. For this, we used only specimens from the Upper Awash Valley (Koka Lake area and Awash National Park). The first component accounts for 39.9% of the total variation, the second one accounts for more 13.1%. The scatter plot of the first two principal components (Fig. 5) shows *Mastomys* n. sp. and *M. erythroleucus* are clearly separated.

So, these analyses indicate unambiguously three *Mastomys* species to occur together in the Upper Awash Valley that are distinguished biometrically.

Description of the new species

Mastomys awashensis Lavrenchenko, Likhnova, and Baskevich, n. sp.

Mastomys sp. 2, LAVRENCHENKO et al. 1992: 90; LAVRENCHENKO and BASKEVICH 1996: 278.

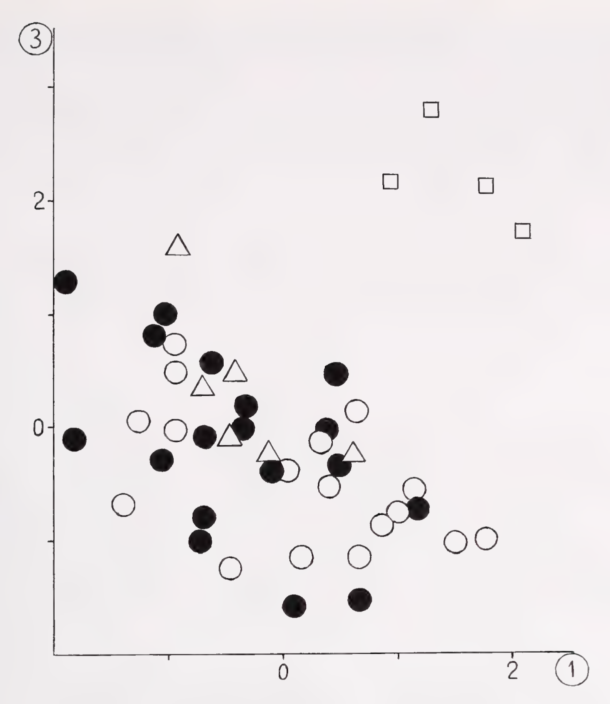


Fig. 4. Bivariate scatter plot of relative positions of specimens of the three *Mastomys* species from the Ethiopian Rift Valley in the projection of principal components I and III. *M. erythroleucus*: localities 2 (empty circles) and 6 (black circles); *M. natalensis*: locality 2 (squares); and *M. awashensis*: localities 1, 2 (triangles).

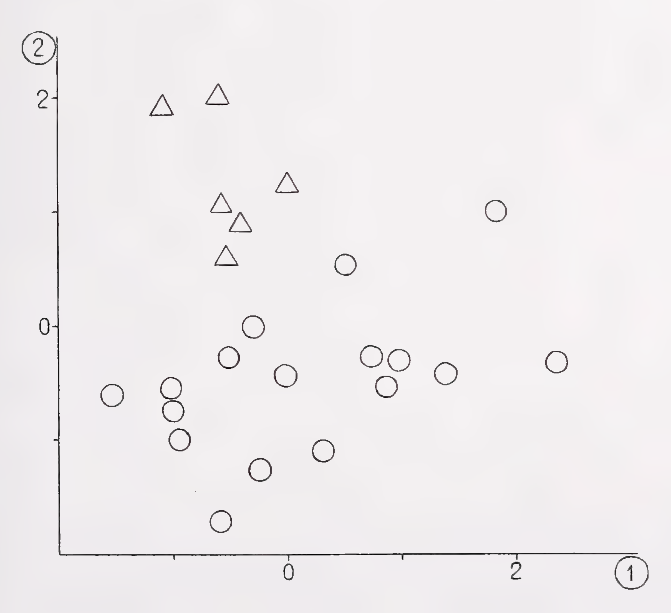


Fig. 5. Bivariate scatter plot of relative positions of specimens of two *Mastomys* species from the Upper Awash Valley in the projection of the first two principal components. See Fig. 4 for symbols.

Holotype: Adult female fixated in formalin and then preserved in alcohol collected at the bank of the Awash River near Koka Lake, Ethiopia (08°23′N 39°09′E) on the 15th May 1990 by Dr. Boris Abaturov. In the collections of ZMMU, No. S-151 552.

Paratypes: More 5 specimens from the same locality Nos. S-151 550 (ZMMU) and 480, 481, 482, 503 (NHMAA); 4 specimens from Awash National Park (09°00′N 40°10′E), collector's Nos. 205, 206, 212, 213 (NHMAA).

Etymology: The species is named after the Awash River, the type locality of the new taxon.

Diagnosis: Typical representative of the *M. natalensis* species complex, similar in size to *M. erythroleucus* but with relatively shorter tail bearing smaller scales (Fig. 6).

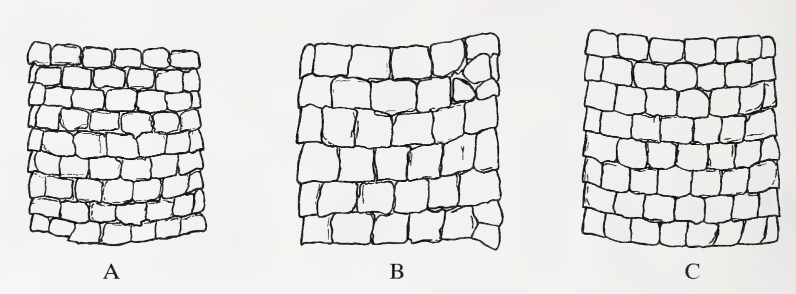


Fig. 6. Tail scales of Ethiopian *Mastomys*. A – *M. awashensis* n. sp. (holotype S-151 552, ZMMU); B – *M. erythroleucus* (S-151 555, ZMMU); C – *M. natalensis* (235, laboratory of mammal microevolution, Institute of Ecology and Evolution RAS). Scale bar = 1 mm.

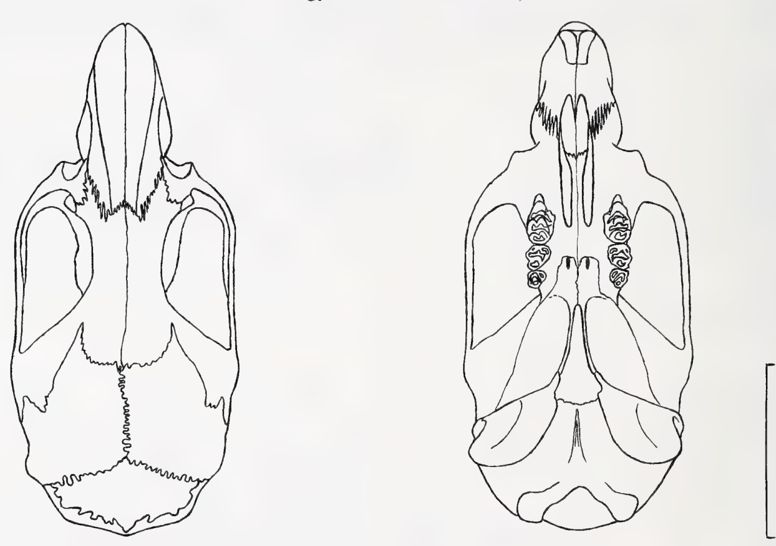


Fig. 7. Skull (dorsal and ventral view) of *Mastomys awashensis* n. sp. (holotype). Scale bar = 10 mm.

Description: *Mastomys awashensis* n. sp. has a pelage coloration that is blackish on the back, with greyish-rufous flanks. The line of demarcation between narrow rufous band on the flank and greyish belly is generally conspicuous. The head is blackish dorsally, with yellowish-rufous cheek: Dorsal side of the hands and feet is white, the claws are light. The skull (Fig. 7) with straight and strongly rounded dorsal edge of anterior margin of zygo-

Table 2. External and cranial measurements (in mm) of adult *Mastomys* from Ethiopian Rift Valley (upper lines:means and standard errors; lower lines: ranges). See text for abbreviations of measurements

Symbole	holotype S-151552	*M. awashensis* (n = 6)	*M. erythroleucus* (n = 35)	*M. natalensis* (n = 4)
L	117.0	121.7 ± 1.97 116.0–127.0	127.8 ± 1.80 103.9–145.0	132.3 ± 4.11 123.0–143.0
C	120.0	118.2 ± 2.01 111.0–123.0	129.3 ± 1.62 111.7–148.0	121.0 ± 4.51 114.0–134.0
Pl	23.5	23.8 ± 0.14 23.5–24.3	24.1 ± 0.20 22.0–26.5	23.9 ± 0.31 23.1–24.5
Au	18.1	19.0 ± 0.31 18.1–20.2	18.5 ± 0.18 16.0–20.3	19.1 ± 0.97 17.0–21.3
Cb	29.8	29.8 ± 0.25 28.8–30.7	30.2 ± 0.25 27.7–33.4	31.9 ± 0.39 30.8–32.7
LoNos	13.5	12.9 ± 0.19 12.2–13.5	13.2 ± 0.14 11.2–14.8	14.1 ± 0.19 13.7–14.4
LoFr	11.0	10.1 ± 0.27 9.0–11.0	9.8 ± 0.14 8.2–11.4	11.1 ± 0.10 10.8–11.3
LoPar	5.2	5.9 ± 0.18 5.2–6.3	5.7 ± 0.08 4.6–6.3	5.9 ± 0.20 5.3–6.2
LoFIn	8.3	7.9 ± 0.09 7.7–8.3	7.6 ± 0.12 6.0–8.7	7.3 ± 0.03 7.3–7.4
LoDia	8.8	8.8 ± 0.13 8.5–9.4	8.6 ± 0.09 7.6–9.8	9.7 ± 0.10 9.4–9.9
LoM^{1-3}	5.4	5.2 ± 0.05 5.1–5.4	5.2 ± 0.02 4.9–5.5	5.6 ± 0.04 5.5–5.7
LaNos	3.4	3.6 ± 0.10 3.2–3.9	3.4 ± 0.03 3.1–3.8	3.6 ± 0.04 3.4–3.6
LaZig	13.5	14.6 ± 0.30 13.5–15.6	15.2 ± 0.13 13.9–16.6	16.4 ± 0.10 16.2–16.6
Lars	0.90	0.85 ± 0.03 0.75–0.93	0.81 ± 0.02 0.65–1.07	1.00 ± 0.04 0.91–1.09
Laaz	1.25	1.22 ± 0.01 1.16–1.25	1.17 ± 0.02 1.00–1.35	1.50 ± 0.04 1.42–1.58
LaIor	4.2	4.6 ± 0.08 4.2–4.8	4.5 ± 0.03 4.2–4.8	4.6 ± 0.03 4.5–4.6
LoMd	18.2	17.9 ± 0.10 17.5–18.2	18.2 ± 0.16 15.9–20.4	20.2 ± 0.12 19.9–20.3
LoM_{1-3}	5.1	4.9 ± 0.05 4.8–5.1	4.9 ± 0.03 4.6–5.2	5.0 ± 0.07 4.9–5.2
LoM_3	1.30	1.22 + 0.03 1.08–1.30	1.19 + 0.01 1.05–1.34	1.40 + 0.05 1.33–1.55

matic plate, narrow mesopterygoid fossa, anterior palatine foramina extending to middle of M^1, palatine bone reaching no further forward than the middle of M^2. Tubercles t 1 and t 4 of the upper first molars are clearly compressed. Cusp t 4 of M^2 is large and lies more or less in line with the second lamina, t 3 of M^2 is reduced and lies in line with t 1 and t 5.

On average, the new species is smaller than *M. natalensis* from the Upper Awash Valley (Tab. 2). The differences are statistically significant for all skull measurements with the exception of LoPar, LaNos, LaIor and LoM_{1-3}. On the contrary, tail length is the only measurement discriminating *M. awashensis* from *M. erythroleucus* from the same area ($t = 2.77$, $P = 0.009$).

The new species differs from *M. erythroleucus* and *M. natalensis* both in its genital morphology and spermatozoal structure (Lavrenchenko and Baskevich 1996) and by fixed alleles at Ldh-B and Got-1 loci and also by Hbb pattern. The karyotype of *M. awashensis* (2 n = 32, NFa = 54) which is similar to that of *M. natalensis* demonstrates, nevertheless, a number of unique characteristics differing it from any known representative of the *M. natalensis* species complex.

Distribution: At present, according to available data, the new *Mastomys* species is confined to a small part of the Upper Awash Valley. All known specimens were captured at two sites: eastern bank of Koka Lake and Awash National Park. We failed to trap any *Mastomys* in the area along the Awash River northward from Awash National Park to Gewane area (10°05′ N 40°33′ E) during 1988–1995 field seasons. Most probably, this area is too arid for any representatives of the *M. natalensis* species complex. On the other hand, Dorst (1972) believes that three sympatric *Mastomys* species occur at the northern bank of Lake Abaya (Merab Abaya: 06°27′ N 37°48′ E). These species might be *M. erythroleucus*, *M. natalensis*, and *M. awashensis*, although we found only *M. erythroleucus* in the neighbouring area (Nechisar National Park: 05°53′ N 37°38′ E) in 1993.

Habitat: The new species inhabits Awash riverbank covered by natural vegetation (Acacia-Commiphora thornbush with high grass) and adjacent agricultural lands. Six other rodent species *Tatera robusta* (Cretzschmar, 1830), *Acomys* sp., *Arvicanthis dembeensis* (Ruppell, 1842), *Praomys fumatus*, *Mastomys erythroleucus*, and *M. natalensis* were captured at the same localities. *M. awashensis* appeared to be outdoor occupant only, whereas the two other Ethiopian *Mastomys* species were found both in natural habitats, agricultural lands, and in the buildings of human settlements.

Discussion

All three Ethiopian multimammate rats considered above belong to the *M. natalensis* species complex, a recently evolved lineage of *Mastomys* which is characterized by larger size of molars and labio-lingual compression of dental tubercles (Denys and Jaeger 1986). Peculiar characteristics of these species exhibit apparent lack of congruence between morphological, allozymic, and chromosomal data. Thus, *M. erythroleucus* and *M. natalensis* share a common genital morphology, differing from that of *M. awashensis* (Lavrenchenko and Baskevich 1996). On the other hand, *M. awashensis* is most closely related to *M. erythroleucus* according to allozymic and morphometric data. Conversely, *M. awashensis* is more similar to *M. natalensis* with respect to chromosomal characteristics (2 n, NFa) and the size of tail scales. This disparity supports our previous supposition about a “mosaic” pattern of evolution under diversification in the *M. natalensis* species complex (Lavrenchenko and Baskevich 1996).

Of three *Mastomys* species occurring in Ethiopia, two (*M. natalensis* and *M. erythroleucus*) are widely distributed throughout the most part of Western, Central, and Eastern Africa. The third one, *M. awashensis*, was found in a restricted area of the Upper Awash Valley. This distribution closely matches the distribution pattern of another

species, 68-chromosomal *Acomys* sp. (Sokolov et al. 1993). Yalden and Largen (1992), in their review of endemic mammals of Ethiopia, claimed that all indubious endemics of this country are rather strictly associated with open habitats at high altitude (19 species) or with remnant forests (9 species). It has been considered that Awash Valley and other Ethiopian dry lowlands are not the most likely habitats for the occurrence of endemic mammals (Yalden and Largen 1992). Our findings of *Mastomys awashensis* and *Acomys* sp. (2 n = 68) show that the Upper Awash Valley with its unique rodent fauna is an integral part of the Ethiopian region with high faunistic diversity and endemism.

The newly described *M. awashensis* must be classified as Vulnerable (VU), criterion D-2 (IUCN Red List Category) because of the small area of its occurrence, the agricultural development of this area, and the non-commensal life style. However, it is difficult to assess what conservation measures might be necessary for this new Ethiopian endemic species without gathering further information on its population levels and habitat requirements.

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Zusammenfassung

Systematik und Verbreitung von Mastomys (Muridae, Rodentia) in Äthiopien mit Beschreibung einer neuen Art

Es wurde die morphologische, allozymische und chromosomale Variation von drei äthiopischen *Mastomys*-Arten aus dem *M. natalensis*-Komplex untersucht. Eine neue Art *Mastomys awashensis* n. sp. wird beschrieben und verglichen mit den anderen beiden *M. erythroleucus* und *M. natalensis.* Diese sind auch in großen Teilen des westlichen, zentralen und östlichen Afrika weit verbreitet. *Mastomys awashensis* n. sp. ist hingegen endemisch im äthiopischen Rift-Tal und wurde dort nur von zwei Örtlichkeiten des oberen Awash-Tales bekannt. Diese neu beschriebene Art unterscheidet sich von den anderen beiden äthiopischen *Mastomys*-Arten durch fixierte Allele an den Loci Ldh-B und Got-1 sowie durch Hbb-Muster und einen relativ kürzeren Schwanz mit kleineren Schuppen. Weiterhin können die drei Arten mit gemeinsamem Vorkommen im mittleren Rift-Tal biometrisch nach multivariater Analyse von Körper- und Schädelmaßen unterschieden werden. Der Karyotyp von *M. awashensis* (2 n = 32, NFa = 54), der dem von *M. natalensis* ähnelt, zeigt dennoch eine Anzahl von eigenen Charakteristika, die ihn von allen anderen bekannten Repräsentanten des *M. natalensis*-Komplexes unterscheidet. Die mit verschiedenen Methoden erhobenen Befunde lassen eine „mosaikartige“ Evolution mit divergenter Radiation in dieser Artengruppe vermuten.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Host chromosomal evolution and parasites of the house mouse *Mus musculus domesticus* in Scotland

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Parasitological studies in the hybrid zone between *Mus musculus musculus* and *M. m. domesticus* (sensu Auffray et al. 1990 and Boursot et al. 1993) showed that the resistance to oxyuroids (*Aspiculuris tetraptera* Schulz, 1924 and *Syphacia obvelata* Rudolphi, 1802) is determined by different genetic systems in each subspecific genome (Sage et al. 1986; *Moulia* et al. 1991, 1995). These studies underlined that pinworms may constitute good markers to distinguish between recently evolved groups such as chromosomal races.

This study focuses on chromosomal races of the house mouse occurring in northern Scotland and in the Orkney archipelago (Fig. 1). Previous cytogenetic analyses in northern Scotland (Searle 1991; Searle et al. 1993) have demonstrated a staggered hybrid zone between a chromosomal race homozygous for metacentrics Rb(4.10), Rb(9.12), Rb(6.13), and Rb(11.14) ($2n = 32$) and the standard race ($2n = 40$). In the center of this zone most individuals are homozygous for two metacentrics Rb(4.10) and Rb(9.12) ($2n = 36$) (Fig. 1). As this 36-chromosome karyotype is common over a large area ($100\ km^2$), it has been suggested that these individuals may constitute a distinct third chromosomal race (Searle et al. 1993). Two alternative scenarios may explain the distribution of these three races. One is that the 36-chromosome form originally occupied the county of Caithness, within which the 32-chromosome race arose in the North-eastern part of this range, as a result of the fixation of two new metacentrics. The second scenario proposes that the 36-chromosome race arose by "zonal raciation" (Searle 1991, 1993) following a secondary contact between the 32-chromosome and the standard races.

Chromosomal races are also found on three islands of the Orkney archipelago (Adolph and Klein 1981; Berry et al. 1992): Westray ($2n = 36$; homozygous for Rb(4.12) and Rb(6.14), Eday ($2n = 34$; homozygous for Rb(3.14), Rb(4.10) and Rb(9.12)) and Faray ($2n = 34$–36; homozygous for Rb(3.14) and Rb(9.12), polymorphic for Rb(4.10) (Fig. 1). Genetic investigations suggest that the various Scottish chromosomal races (mainland and islands) are probably closely related and share a common origin (Nash et al. 1983).

Here we report the first attempt to distinguish between chromosomal races of the house mouse (*M. m. domesticus*) using a parasitological approach.

One hundred and sixty-six house mice from the three mainland races were collected during two field trips (24 March–10 April and 15–23 September 1992; Fig. 1; for further details see Ganem et al. 1996). Eighty seven animals from four island populations (Papa-Westray, Sanday, Eday, Westray; Fig. 1) were trapped during late February–April 1992.

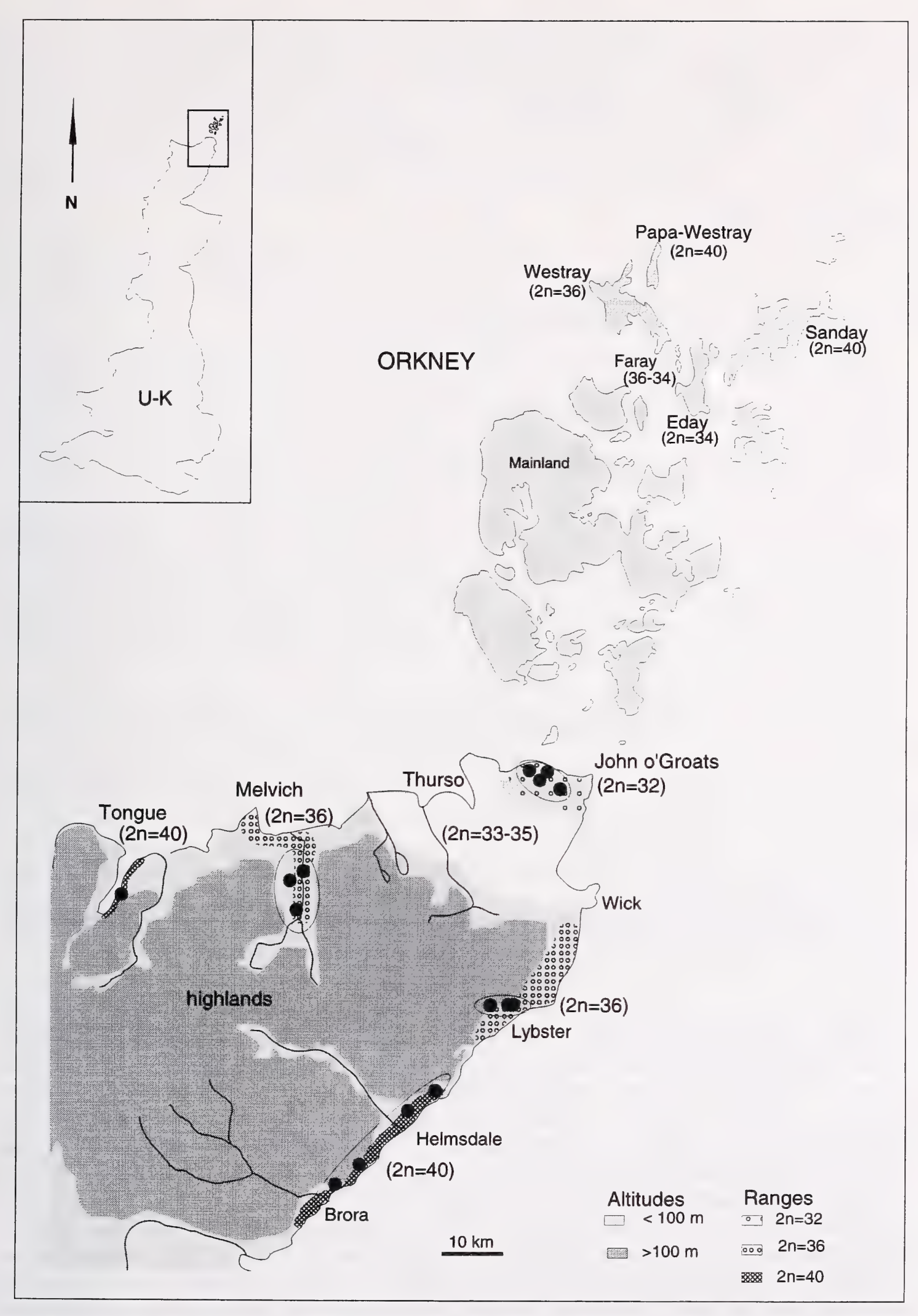


Fig. 1. Geographic location of the different chromosomal zones described in this study. The mice from mainland Scotland used for the parasitological analysis came from the sites marked by closed circles. Pooled localities are indicated and their mean diploid provided. Mice with reduced chromosome numbers are almost completely limited to Caithness, which forms a boundary with Sutherland along a line approximately between Melvich and Helmsdale.

Only adults were kept in the laboratory to study behaviour (GANEM and SEARLE 1996 a, b) and parasitology (this study). They were maintained in male-female pairs for 3–4 months in the same animal room and under standardised conditions. Because pregnancy may modify the immune and parasitological state, females that became pregnant were excluded from the parasitological study. When mice were killed, their karyotypes were prepared. The intestines of each mouse were dissected and the nematodes isolated under a binocular microscope. Parasite loads were estimated by counting all oxyuroids without distinguishing species.

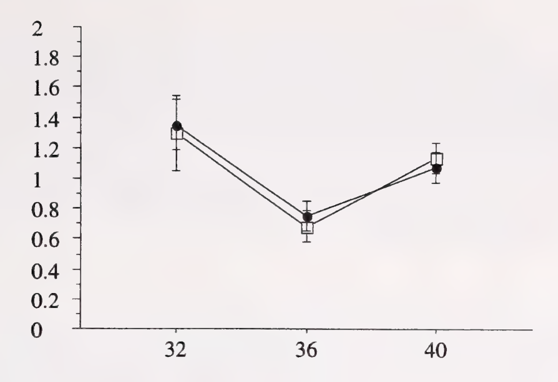
Data on parasite loads were log-transformed for homoscedasticity (Bartlett's test: $\chi^2 = 2.26$, d. f. = 5, $p < 0.01$). An analysis of variance was applied to the transformed data and a Student-Newman-Keuls (SNK) test was used as a posthoc test for multiple comparisons between samples (SCHERRER 1984; SOKAL and ROHLF 1995).

Mainland and island mice were divided into three groups according to their karyotype (mainland: 2 n = 32, 2 n = 36, 2 n = 40; islands: 2 n = 34, 2 n = 36, 2 n = 40). Differences between karyotypes from mainland and island samples were tested separately. A three-way Anova with karyotype, season, and sex as main factors showed a significant effect of karyotype on the mainland ($F_{2,154} = 10.5$, $p = 0.0001$): mice of the 36-race displayed the lowest parasite load and mice from the 32 and 40-races the highest (SNK post-hoc tests: 36–40: $p < 0.01$; 36–32: $p < 0.01$; 40–32: $p > 0.05$; Fig. 2 a). Similarly, within the island sample, mice of the 36-race showed the lowest parasite load ($F_{2,81} = 11.6$; $p = 0.0001$; 36 i–40 i: $p < 0.05$; 36 i–34 i: $p < 0.01$; 34 i–40 i: $p > 0.05$; Fig. 2 b). However, a sex effect was detected in the island sample ($F_{1,81} = 10.4$, $p = 0.002$) due to a lower parasite load in the standard-type females than in the males ($t = 2.46$, d. f. = 35, $p = 0.02$; Fig. 2 b). Nevertheless, on average, both mainland and island standard race mice show similar susceptibilities ($t = 0.02$, d. f. = 115, $p > 0.05$).

The long period of laboratory standardisation is believed to minimise environmental effects (i. e. site, season) on the parasitological state of each individual. Indeed, even if housed in different cages, mice are easily contaminated by pinworm eggs from infested individuals occurring in the same room. Moreover, the oxyuroids have a direct cycle with pre-patent periods no longer than three weeks. Therefore, during the 3–4 month period in the laboratory, each mouse could have been challenged to several reexposures to these parasites (SCOTT and GIBBS 1986). The fact that there was no seasonal variation between the mainland samples ($F_{1,154} = 2.1$, $p > 0.05$) strongly supports this proposal. Thus, our results reflect to a large extent the occurrence of variation in resistance to pinworms in the different chromosomal races of the house mouse in northern Scotland.

Only one race (the island standard-type) displays sex differences in its infestation level due to a higher parasite load in the males. Such a phenomenon has been reported, although in a different context, for other wild rodent populations (BEHNKE 1975). In the present study, the sample size may not have been sufficient to detect such microvariation within the other races. However, given that male-enhanced susceptibility can depend on the immunomoduling effect of testosterone (ALEXANDER and STIMSON 1988; ZUK 1990), an additional hypothesis may be that male mice in the two island standard-race populations have higher basal levels of testosterone than those in the other populations. A more detailed study should clarify this point.

The most striking result of this study concerns the resistance of the 36-chromosome races when compared to the standard and 32- or 34-races. Among the two scenarios explaining the origin of the 36-chromosome mainland race, the parasitological results are consistent with a hybrid origin. The reduced susceptibility to pinworms of this race would be related to "outbreeding vigour" due to the increased polymorphism generated by divergence of the parental races. These results contrast with the enhanced susceptibility of hybrids between *M. m. domesticus* and *M. m. musculus* (MOULIA et al. 1991, 1993), but do not contradict it. In this case, the apparent "outbreeding depression" would result from



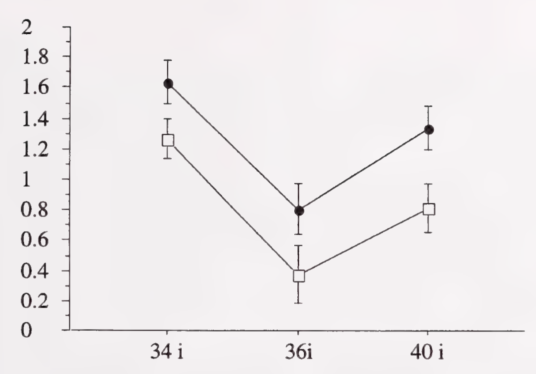


Fig. 2. Mean (+/– s. e.) parasite load (P. L.) of each sample of chromosomal race. 2 a: mainland Scotland: male (●) and female (□) P. L. are shown independently (non-significant difference). 32, 36, 40 refer to 32-, 36- and 40-chromosome races respectively. 2 b: Orkney's islands: male (●) and female (□) P. L. are shown independently (significantly different, see text); 34 i, 36 i et 40 i refer to 34-, 36- and 40-chromosome island races.

the accumulation of incompatible alleles in the two subspecies (Orr 1995). Additional support for the hybrid origin hypothesis is provided by the intermediate pattern in behavioural divergence shown by the mainland 36-chromosome race when compared to the other two mainland races (Ganem and Searle 1996 a, b).

The alternative hypothesis, i. e. the 32-race arose within the 36-race, is much less likely since it would imply that the 32-chromosome mice developed a higher susceptibility than the putative parental mice and yet still managed to prosper and expand their range.

The similarities in parasite resistance between both the mainland and the island 36-races is puzzling. Indeed, the two races occupy different geographic areas and share only one metacentric, Rb(9.12), which is also present in the other chromosomal races analysed in this study. Even if the various Scottish chromosomal races share a common origin (Nash et al. 1983; Davis 1983), the mainland and island 36-chromosome mice have most likely experienced different histories, suggesting that parasite resistance in these two races most likely evolved through different evolutionary processes. One possible explanation lies in the founding of the initial Westray 36-chromosome population by resistant individ-

uals. Alternatively, resistance to pinworms in this island chromosomal race may have arosen through a hybridisation event as in the mainland 36-race. To determine the origin of resistance in these mice will require extending the parasitological analysis to other island populations of the archipelago and clarifying the genetic relationships of these mice using molecular markers.

Although, these preliminary results need to be confirmed by controlled infestations in laboratory, they do suggest that the parasitological approach may open new perspectives in the field of chromosomal evolution.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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WISSENSCHAFTLICHE KURZMITTEILUNG

Holocene variation in the small mammal fauna of central Chile

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The species composition of contemporary communities is a recent phenomenon emerging from the individualistic response of each species to changing environmental conditions (GLEASON 1926). Changes in species composition varies at different time and spatial scales. Therefore, understanding of contemporary communities requires to place the local community in its historical and biogeographical context (RICKLEFS and SCHLUTTER 1993).

Contemporary small mammal assemblages have fewer species than those of recent past. Chilean caviomorph assemblages are depauperated and nested subsets of past faunas (SIMONETTI 1994). Local extinctions during the Holocene determined that current distributional ranges were attained recently, following a more widespread distribution of several taxa (SAAVEDRA et al. 1991; SIMONETTI and SAAVEDRA 1994). The early Holocene caviomorph assemblages of the Andes of central Chile comprised six species, two becoming locally extinct around 1,500 years BP. Nevertheless, the generality of the Holocene reduction in species richness in central Chile needs to be established. Here, we further analyze the late Holocene dynamics of caviomorph assemblages in the Coastal Range of central Chile, and compare it to that of the Andean range (SIMONETTI 1994). If species impoverishment is a general event, past assemblages at the Coastal Range ought to be richer than current ones, following a similar trend of species depauperation than in the Andes. Furthermore, we will examine whether changes occurred simultaneously or if they vary geographically.

New samples of the Coastal Range come from prehistoric rodent assemblages recovered in three archaeological sites located in Las Chilcas (Las Chilcas 1: 32°53′ S, 70°49′ W, Las Chilcas 2: 32°51′ S, 70°52′ W, and Piedra del Indio: 32°54′ S, 70°48′ W, Fig. 1). These sites are small rockshelters, were humans and owls deposited small mammal remains among other biological and cultural material (SAAVEDRA 1997; see HERMOSILLA 1997; HERMOSILLA et al. 1997a for excavation and recovery details). Species were considered attributes of the sample, considering only their presence-absence pattern (GRAYSON 1984). Past assemblages from Las Chilcas area were compared to present day ones as well as past assemblages from El Manzano basin (34°34′ S, 70°24′ W). Contemporary species composition for an area of 4 km around rockshelters was assessed from literature records, live trapping around rockshelters, sightings, and from prey remains of local predators (the owls *Tyto alba* (Scopoli, 1769) and *Bubo virginianus* (Gmelin, 1788) and the fox *Pseudalopex* sp.).

A total of 21,459 bone specimens of small mammals was recovered. However, only 4,164 were identifiable to the family level. From these, 2,619 (63%) were from four caviomorph species: *Abrocoma bennetti* Waterhouse, 1837, *Octodon bridgesi* Waterhouse, 1895, *Octodon degus* (Molina, 1782), and *Spalacopus cyanus* (Molina, 1782) (Tab. 1). Las Chil-

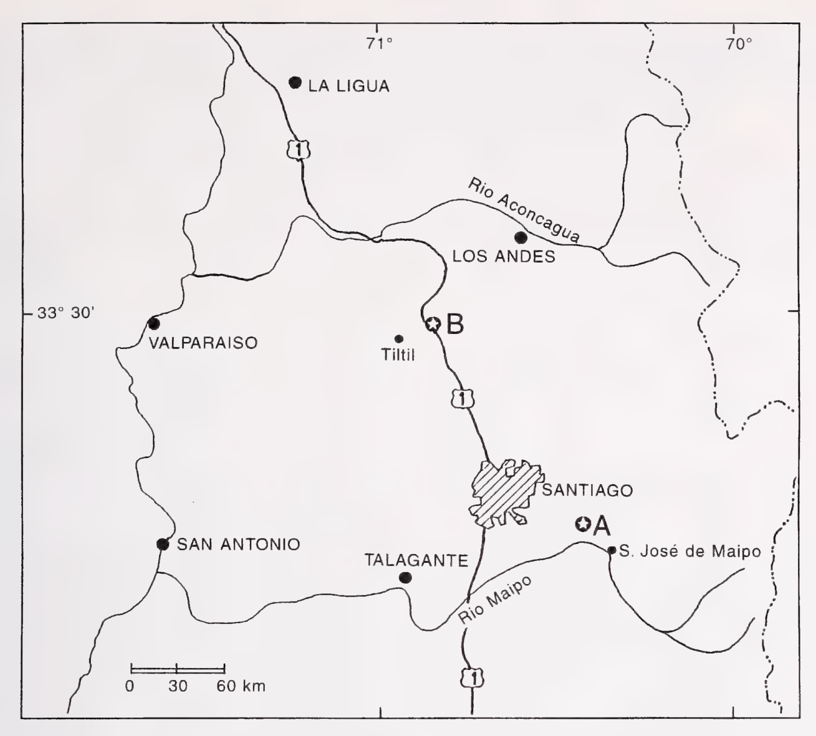


Fig. 1. Locations of sites sampled. The three rockshelters of Las Chilcas area are shown together (B) as well as the two rockshelters at El Manzano basin (A).

cas 1 rockshelter yielded a sequence of 2,800 years. A total of 1,206 caviomorph specimens was recovered from the four caviomorph species (Tab. 1). Other species recovered were *Abrothrix* sp., *Oligoryzomys longicaudatus* (Bennet, 1832), and *Phyllotis darwini* (Waterhouse, 1837), all myomorphs. They were not included in our analysis due to their low sample size (combined NISP = 129). At Las Chilcas 2, a sequence of at least 2,000 years was established. Here, 633 specimens of the same four caviomorph species were retrieved (Tab. 1), together with remains of *P. darwini* and unidentified cricetids (NISP = 75), that were excluded from our analysis. At Piedra del Indio, the sequence embraces at least 1,200 years, with 780 caviomorph remains recovered (Tab. 1) together with *O. longicaudatus* and *P. darwini* (combined NISP = 34), also excluded from the present analysis.

The three sites shared four caviomorph species, being present from 2,800 to 160 years BP. Only one species, *O. bridgesi* disappeared, around 160 years BP (Tab. 1). Currently, this species does not inhabit the area, as assessed by published records (Redford and Eisenberg 1992), live trapping and predator diets. Only *A. bennetti*, *O. degus*, and *S. cyanus* have been recorded in the area. Comparing the same period of time, from 2,500 years ago onward, the fauna of Las Chilcas holds fewer species compared with El Manzano basin, where *Aconaemys fuscus* and *Lagidium viscacia* were present at different times (Tab. 1, Simonetti and Saavedra 1994; Simonetti 1994). *Aconaemys fuscus* disappeared from El Manzano only in recent times, and is now distributed in Chile between 35° and 40° S (Contreras et al. 1987), two degrees south of their past distribution. *Octodon bridgesi*, an habitat specialist, persisted up to 160 years BP in Las Chilcas, but at El Manzano basin it disappeared by 1,500 years BP (Tab. 1; Simonetti and Saavedra 1994; Simonetti 1994).

Table 1. Species composition of caviomorph assemblages from the coastal range (Las Chilcas 1, Las Chilcas 2, and Piedra del Indio) and the Andean range (El Manzano 1 and La Batea 1, from SIMONETTI 1994) of central Chile. Abbreviations: *Aben*, *Abrocoma bennetti*; *Afus*, *Aconaemys fuscus*; *Obri*, *Octodon bridgesi*; *Odeg*, *O. degus*, *Scya*, *Spalacopus cyanus* and *Lvis*, *Lagidium viscacia*. nisp is the number of identified specimens.

SITE/STRATUM OR DATE (years B.P.)	*Aben*	*Afus*	*Obri*	*Odeg*	*Scya*	*Lvis*
Las Chilcas 1						
Present	•			•	•	
700	•		•	•	•	
1,420–1,820	•		•	•	•	
1,970	•		•	•	•	
2,790				•	•	
Total nisp	197		6	775	228	
Las Chilcas 2						
Present	•			•	•	
36–160	•		•	•	•	
undated	•		•	•	•	
2,020	•			•	•	
Total nisp	267		3	355	8	
Piedra del Indio						
Present	•			•	•	
undated	•		•	•	•	
1,240	•			•	•	
Total nisp	45		3	613	119	
El Manzano 1						
Present	•			•	•	•
1,500	•	•		•	•	
undated	•	•	•	•	•	•
undated	•		•	•	•	•
8,900	•	•	•	•	•	•
undated	•	•	•	•	•	
Total nisp	12	14	24	66	99	6
La Batea 1						
Present	•			•	•	•
undated	•	•		•	•	•
1,500	•	•		•	•	•
2,400	•	•	•	•	•	•
4,500	•	•	•	•	•	•
undated	•	•		•	•	•
5,600	•	•		•	•	•
undated	•	•	•	•	•	•
Total nisp	118	44	16	203	359	11

The structure of current caviomorph assemblages in central Chile is a recent phenomenon, originating by a reduction in the number of species from Holocene assemblages, but the time at which current assemblages attained their modern structure varies geographically. While local extinctions shape the structure of modern assemblages, its occur-

rence is heterochronic. This difference could be due to a distinct prehistoric land-use regime. Central Chile was hetereogeneously used by prehistoric people, which could have triggered a mosaic of small mammal assemblages depending on the type and intensity of the land use (SIMONETTI and CORNEJO 1990; CORNEJO and SIMONETTI 1992).

The local extinction of *O. bridgesi* at El Manzano has been attributed to human disturbance of its habitat. This species inhabits only dense woodlands, which were cleared by prehistoric people to prepare landfields for horticulture. The disappearance of this species at El Manzano basin coincides with the settlement of horticulturists in the area, which was persistently used for over 9,000 years (SIMONETTI and CORNEJO 1990; CORNEJO and SIMONETTI 1992; SIMONETTI 1994). In contrast to El Manzano, Las Chilcas never supported a resident human population, being an area marginally used as a stopover while moving between adjacent basins or in an Andes-coast circuit (HERMOSILLA et al. 1997b); that is, under reduced human pressure, *O. bridgesi* persisted until modern times. Its more recent extinction could be associated to the increased use of the Coastal Range during the 18th and 19th centuries, when it was more intensively used as a source of fuel wood for mining as well as wheat production to supply Californian and Australian gold miners (ASCHMANN 1991). Wood cutting for mining and land clearing could have modified the dense habitat preferred by *O. bridgesi* as prehistoric settlers did in past times at El Manzano.

The heterogeneity in the timing of the faunal changes is related to differential patterns of prehistoric land use, generating a mosaic of impacts and assemblages across the space and time. To ignore the vicissitudes of this fauna may lead to equivocal interpretations about the discrepancies in convergent evolution in Mediterranean ecosystems. Regarding small mammals, central Chile is considered poor in species compared to California (GLANZ 1977). However, when extinct species are taken into account, differences are greatly reduced. Therefore, discrepancies are recent and the result of the long-term human intervention of the habitat (SIMONETTI 1994). Recently, a debate arose concerning the causes for the depauperate condition of small mammal fauna of central Chile. Based on cricetid species, isolation versus aridity is argued as the key factor shaping a species-poor fauna (CAVIEDES and IRIARTE 1989; MESERVE and KELT 1990). These claims ought to be re-evaluated as richer and more complex assemblages than previously known inhabited central Chile during the Holocene. Clearly, if the structure of modern assemblages is to be understood, both modern and past distributions must be known. Prehistoric land use has affected the local distribution of several taxa and the structure of assemblages from tropical, temperate and to Mediterranean regions (e. g. BLONDELL and VIGNE 1993), and Chile is not an exception. As for contemporary caviomorph assemblages, they not only are a recent biological phenomena but also reflect long-term human impact which are heterochronic at different localities in central Chile.

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MITTEILUNGEN DER GESELLSCHAFT

72. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde vom 20.–24. September 1998 in Prag

Einladung

Auf Einladung des Dekans der Naturwissenschaftlichen Fakultät der Karls-Universität zu Prag, Prof. Dr. Sc. Karel Štulik und von Herrn Doz. Dr. Leo Sigmund, Department of Zoology, findet die 72. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde e. V. von Sonntag, dem 20. September, bis Donnerstag, dem 24. September 1998, an der Karls-Universität zu Prag statt. Die Tagung ist Teil eines umfangreichen Festprogramms anläßlich des 650. Jahrestages der Gründung dieser traditionsreichen Universität.

Vorläufiges Programm

Sonntag, 20. September:
Anreise
ab 16.00 Uhr: Vorstandssitzung
ab 19.00 Uhr: Zwangloser Begrüßungsabend

Montag, 21. September:
09.00 Uhr: Hörsaal des Karolinums: Grußworte der Gastgeber und Eröffnung der Tagung durch den Vorsitzenden
09.30 Uhr: Hauptvortrag (F. Spitzenberger, Wien) und Kurzvorträge zum Themenschwerpunkt „Biodiversitätsforschung“
14.00 Uhr: Posterdemonstration
15.00 Uhr: Kurzvorträge
16.00 Uhr: Mitgliederversammlung
19.00 Uhr: Führung durch das Nationalmuseum durch den Leiter der Zoologischen Abteilung, M. Andera

Dienstag, 22. September:
09.00 Uhr: Hörsaal des Karolinums: Hauptvortrag (W. Maier, Tübingen) und Kurzvorträge zum Themenschwerpunkt „Morphologie“
14.00 Uhr: Posterdemonstration
15.00 Uhr: Kurzvorträge
19.30 Uhr: Festliches Konzert und geselliger Abend in den Repräsentationsräumen des Karolinums

Mittwoch, 23. September:
09.00 Uhr: Hörsaal des Karolinums: Hauptvortrag (P. Vogel, Lausanne) und Kurzvorträge zum Themenschwerpunkt „Biologie der Insectivora“
14.00 Uhr: Posterdemonstration
15.00 Uhr: Kurzvorträge
18.00 Uhr: Posterprämierung

Donnerstag, 24. September:
09.00–18.00 Uhr: Exkursion
09.00 Uhr: Department of Zoology der Karls-Universität: Workshops/Symposien der Arbeitsgruppen

Alle Interessenten, Mitglieder und Nichtmitglieder, sind zu dieser Jahrestagung 1998 der Deutschen Gesellschaft für Säugetierkunde in Prag herzlich eingeladen. Kongreßsprachen werden Deutsch und Englisch sein. Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt. Sollten Sie eine persönliche Einladung benötigen, so wenden Sie sich bitte direkt an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. H. Erkert, Zoologisches Institut, Morgenstelle 28, D-72076 Tübingen (Tel. 0 70 71/ 2 97 29 58; Fax-Nr. 0 70 71/29 46 34).

Wir bitten um die Anmeldung von Tagungsbeiträgen. Außer Beiträgen zu den genannten Themenschwerpunkten werden auch dieses Mal wieder verstärkt Kurzvorträge und Posterdemonstrationen zu anderen Fachgebieten der Säugetierkunde berücksichtigt.

Bitte melden Sie Kurzvorträge (15 min + 5 min Diskussion) sowie Posterdemonstrationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer der DGS, Prof. Dr. R. Schröpfer, Fachbereich Biologie/Chemie, Barbarastr. 11, D-49069 Osnabrück (Tel. 05 41/9 69-28 48, Fax: 05 41/9 69 28 62) an. Der Anmeldung ist eine maximal einseitige informative Kurzfassung (1,5zeilig) beizufügen. Aus ihr sollten die Fragestellung, Methoden, Ergebnisse und die daraus gezogenen Schlußfolgerungen hervorgehen. Alle angenommenen Kurzfassungen werden wieder in einem Sonderheft der Zeitschrift für Säugetierkunde publiziert. Sie sind nach folgendem Schema abzufassen: Deutscher Titel, Leerzeile, englische Titelübersetzung (kleine Anfangsbuchstaben im Text; bitte ggf. einen „native speaker" konsultieren!), Leerzeile, Initialen und Familienname(n) des/der Autors(in) bzw. der Autoren(innen) in Großbuchstaben, Adresse, Leerzeile, Text). Aus arbeitsökonomischen Gründen bitten wir dringend darum, zusätzlich zum ausgedruckten Abstract möglichst noch eine Fassung auf Diskette (5.25″ oder 3.5″, IBM-kompatibler DOS-PC) in Form eines Word- (5.0 oder 5.5), Word Perfect- (5.1 oder 6.0) oder ASCII-Files mitzuschicken. Bitte formatieren Sie diesen File nicht! Die Maße für Poster werden im Juli-Rundschreiben der DGS bekanntgegeben.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Herrn Doz. Dr. Leo Sigmund, Department of Zoology, Charles University, Vinicná 7, CZ-12844 Prague 2, Czech Republic (Telefon: 00 42/02/21 95 32 61; Telefax: 00 42/02/21 95 32 67).

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Einsendung und Annahme von Manuskripten: Ms. zur Veröffentlichung sind einzusenden an den 1. Schriftleiter: Herrn Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel. e-mail: dkruska@ifh.uni-kiel.de

Über die Annahme von Ms. zur Veröffentlichung wird gemäß Geschäftsordnung der Deutschen Gesellschaft für Säugetierkunde entschieden. Der Eingang von Ms. wird sofort bestätigt, und nach Erhalt der Gutachten werden die Autoren über die Entscheidung umgehend informiert.

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Effects of bat-bands and banding on a population of *Pipistrellus nanus* (Chiroptera: Vespertilionidae) in Malawi

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Abstract

This study provides information about the effects of flanged metal bat-bands, and the procedures associated with banding and frequent censusing, on a population of *Pipistrellus nanus*, a particularly small vespertilionid bat. The bats were censused at their roosts in a banana plantation, at intervals of approximately two weeks, for 10 months; 120 bats were banded and 75 were recaptured (447 recaptures). The best data came from a cohort of 64 adults (banded during the first six censuses), 25 of which were recaptured 9–15 times. Band-status (the effect of the band on the bat) was recorded each time a bat was captured. We recognised four classes of band-status ranging from class 1 (band-free with no injuries, observed on 66% of occasions) to class 4 (band-immobile with an unhealed wound, observed on 11% of occasions). Analyses of the results showed that (a) the majority of bats were in class 1 on most occasions, but some had injuries (classes 2–4) which often improved or deteriorated unpredictably; (b) the band-status changed in relation to time after banding, following an unexplained pattern; (c) band-status was not affected by seasonal changes in climate, or by the sex of the bat; (d) banding did not affect flight and foraging, or mass, or "survival" in the population; and (e) roosting behaviour was not adversely affected. Bats banded when we were inexperienced (census 1) were more prone to injuries than bats banded when we had improved our banding technique. Banding enabled us to study the social behaviour and reproduction of this species and we believe that the results justified banding one small population of this common, widespread species. We predict that other species of small vespertilionids may respond similarly to banding, but extrapolation to species in other families is probably not justified. We recommend that flanged bat-bands should be fitted as loosely as possible, that new bat-banders should be trained by experienced banders, and that banding of bats is permitted only when there are very good scientific reasons for the banding and when harm to individual bats and populations is likely to be minimal.

Key words: *Pipistrellus*, Chiroptera, Bat-bands, banding, techniques

Introduction

Banding of bats, with numbered bands so that individuals may be recognised if recaptured, has been conducted for many years (Barclay and Bell 1988; Greenhall and Paradiso 1968; Roer 1995), and has often yielded valuable information. However, bat-banding has limitations and disadvantages which make its usefulness controversial – both scientifically and ethically. For example, bats must be handled when the band is fitted and

usually have to be recaptured to obtain further data. Both procedures may interfere with the behaviour and well-being of the bats. In addition, bands may cause injuries ranging from trivial to potentially fatal (Bels 1952; Cockrum 1956; Cranbrook and Barrett 1965; Dwyer 1965; Herreid et al. 1960; Hitchcock 1957).

Originally, bats were banded on the hind-foot with conventional bird-bands but, in 1939, Trapido and Crowe (1946) began banding on the forearm, and this method has been widely used ever since (Greenhall and Paradiso 1968). However, bird-bands placed on the wing frequently caused extensive injuries and therefore, about forty years ago, a special flanged metal band ("bat-band") was designed specifically for bats with the object of minimising band-caused injuries (Hitchcock 1957). Bat-bands have been shown to cause fewer injuries than bird-bands (Dwyer 1965; Herreid et al. 1960), but they do cause some injuries, and the banding procedures may still cause distress and the disruption of normal behaviour. Very often, data obtained by banding cannot be fully interpreted unless the effects of the bands and banding procedures are known. In order to assess the effects of the bands and banding the following conditions must be satisfied: the bats must be recaptured frequently over a suitably long period, the fate of bats which are not recaptured must be known, and any changes in behaviour which may be attributable to the bands and banding procedures must be documented. In the field, this is practically impossible. Nevertheless, valuable information about the effects of bands and banding can be obtained if a large percentage of the banded bats are recaptured frequently over a long period, and if it is possible to compare the health and behaviour of banded and unbanded bats (other factors being equal). We were able to obtain this sort of information while studying a population of banana bats, *Pipistrellus nanus* (Peters, 1852) banded with flanged metal bands (Bernard et al. 1997; Happold and Happold 1996). Banana bats are very small vespertilionids with a mass of 2.5 to 5.0 g (mean 3.2 ± 0.5 g, excluding pregnant females) and mean forearm length of 31.5 mm. During the day, they usually roost in the furled leaves of banana plants, and all occupants of a furled leaf can be captured easily (Happold and Happold 1990).

This study provides detailed information and analysis of the effects of flanged metal bat-bands on the welfare and biology of this particularly small vespertilionid bat, and on the procedures associated with banding. The study also considers the situations and conditions for which bat-banding may be justified.

Material and methods

The study was conducted in an isolated plantation of 138 clumps of banana plants on Kapalasa Farm near Namadzi (15°31′ S, 35°11′ E; ca. 1000 m a. s. l.) on the Shire Highlands of Malawi in east-central Africa. The bats were censused at their roosts in the plantation using a modified butterfly net, and it was usually possible to capture every bat which was roosting in the plantation on the day of a census (Happold and Happold 1996). Each bat was weighed to the nearest 0.5 g, and its reproductive condition, roosting associates, band number, and band-status (including injuries and bite marks) were recorded. The bats were released near a swimming pool adjacent to the plantation, usually at dusk when it was still light enough to observe their flight and behaviour. On some occasions, echolocation calls associated with foraging and feeding were recorded and analysed with an Anabat II bat-detector, tape-recorder, Anabat II zero crossings analysis interface module and Anabat II software (Titley Electronics, P. O. Box 19, Ballina, N. S. W. 2478, Australia). The calls of banana bats were recognised by their "shape", and by their minimum and characteristic frequencies. The flight and foraging behaviour of the banded bats was compared with that of unbanded banana bats.

When first captured, each bat was banded by placing a numbered metallic bat-band around the right forearm. We used 2.2 mm alloy bat-bands [Code: IBR 3505, from Lambournes Ltd, Shallowford Court, off High Street, Henley-in-Arden, Solihull, West Midlands B 95 5 BY, England.]. Each band was roughly circular, with outwardly curving flanges at the open end. All edges of the band were rounded

and smooth, and contact between the wing membrane and the band was through the two smooth, broad surfaces of the flanges. The average mass of each band was 0.037 g (manufacturer's information), equivalent to 1.2% of the mean mass of the species (excluding pregnant females) and 1.5% of the mass of the lightest individuals which were banded.

All bands were fitted by one person (D. C. D. H.) although the body and outstretched wing of the bat were supported firmly by M. H. whose hands rested on a bench while the band was being fitted. Neither authors had previous experience at banding bats although they had consulted bat-banding literature and several bat-banders prior to the study. During the first census, the band was carefully placed around the forearm and then squeezed once only (by applying pressure on either side of the band with thumb and index finger) until the gap between the flanges were almost closed. The band was then moved along the forearm to ensure that it slid smoothly over the wing membrane and, in a few cases only, it was necessary to prize the flanges further apart. This method is referred to as Technique A. Approximately half of the bats banded during Census 1 were recaptured at Census 2 (two weeks later) and 38% (n = 32) had bands which had become immobile. Because this was unsatisfactory, we adopted Technique B which aimed at maximising the gap between the flanges. This was achieved by closing the gap by very small increments until it was closed just enough to prevent the band falling off. After each squeeze, the band was gently pulled outwards to ensure that it could not be detached, and then moved up and down the forearm to ensure that it could not slide over the joints. If necessary, the band was given a small extra squeeze and tested again. Technique B usually involved 2–4 squeezes to fit each band satisfactorily.

Censuses were conducted on 18 occasions, at intervals of approximately two weeks, for a period of 41 weeks from late August 1993 to mid-June 1994, except for a period of six weeks (16 November to 29 December) while the females were giving birth and suckling non-volant young. At each census, except Census 6, all furled leaves on the 138 clumps of bananas were examined. Census 6, on 15 November, was terminated when a lactating female was captured.

As in Happold and Happold (1996) this study is divided into four periods. These periods, and the censuses within each period, were:

Period 1: the hot dry season when all females were pregnant; late August to mid-November (censuses 1–6).
Period 2: the hot wet season, when females give birth and lactate and males are in the early stages of spermatogenesis; mid-November to end of April (censuses 7–14).
Period 3: the first half of the cool dry season; spermatozoa are released into the epididymides, and mating begins at the end of the period; May and June (censuses 15–18).
Period 4: the second half of the cool dry season; sperm are stored by both sexes, mating presumably continues, and ovulation and fertilisation occur at the end of the period; July to late August (no censuses).

Bats were assigned to cohorts depending on when they were first caught and their age (adult, young of the year). These cohorts were:

Cohort 1: adult bats banded during Period 1, no young present (n = 84),
Cohort 2: young bats banded in Period 2 (n = 20),
Cohort 3: adult bats banded in Period 3 (n = 21).

Throughout this study, the bands were not damaged by the bats, and therefore the term "band-status" (used below) refers solely to the physical effects of undamaged bands on the wings of the bats. Four classes of band-status were recognised. During each census, the band-status for each captured bat was entered on a conventional calendar of catches (longitudinal data) and on a second calendar of catches laid out according to the number of weeks after the bat was banded (cross-sectional data). Both data sets were analysed using, where appropriate, non-parametric statistics (Kruskal-Wallis and Mann-Whitney U tests). Mean values ± one standard deviation are given where relevant.

During the last census, no bats were banded (although five new bats were captured), and bands were removed from all recaptured bats. Bands were removed very easily by prizing the flanges apart with the thumb-nails while supporting the band with the index fingers. A second person held the bat with its wing outstretched during this procedure.

In addition to the censuses of bats in the Kapalasa plantation, banana bats were caught in mist-nets located at seven localities within a 1.5 km radius from the plantation. Others were taken from furled leaves in the nearest banana plants to the Kapalasa plantation (0.2 to 1.5 km away) and in plantations at Zomba (20 km away). Most of these bats were not banded and they enabled us to compare banded and not-banded bats.

Rainfall and daily maximum and minimum temperatures were recorded throughout the study. Further climatic details are given in Happold and Happold (1990).

Results

Between 27 August 1993 and 13 June 1994, 125 banana bats (50 males, 75 females) were captured in the banana plantation and, of these, 120 were banded. Cohort 1 contained 84 adults (30 males, 54 females) of unknown age which were banded between 27 August and 15 November 1993 (Period 1). Cohort 2 contained 20 young of the year (born about 15 November) which were banded between late December 1993 and March 1994 (Period 2); no new adult bats were caught in Period 2. Cohort 3 contained 21 adults (young of the year which had reached adult size or adults born in previous years) which were banded in April–June (Period 3). The 84 bats of Cohort 1 provided the best data on the effects of the bands and banding procedures for the following reasons. (1) Sixty-four of these bats were recaptured. (2) The number of times males were recaptured ranged from 0–15 (mean 7.2 ± 4.5, $n = 30$), and the number of times females were recaptured ranged from 0–15 (mean 3.6 ± 4.5, $n = 54$). (3) The number of weeks between the first and final times a bat was caught in the plantation ranged from 2–41 weeks with 41 weeks being the maximum possible; however, for 61% of the bats, the range was 28–41 weeks. (4) Twenty-five bats which were recaptured nine or more times over at least 34 weeks provided longitudinal data. (5) The masses of banded and unbanded bats could be compared. Some data were also obtained from the bats of Cohort 2.

Band Status

Description of band-status

Band-status was recorded for each bat on each occasion when it was recaptured (447 recaptures, 75 bats). Four classes of band-status (the effects of undamaged bands on the wings of the bats) were recognised:

Class 1. Band free with no evidence of any injury (past or present).

Class 2. Band free but with slight chafing or inflammation, and/or evidence of more severe injury in the past.

Class 3. Band immobile but surrounded by a wound which was healed. Class 3 status was the result of swelling and/or abrasion which resulted in the band becoming immobilised by dried fluids, scab tissue or, at worst, an over-growth of flesh. Immobile bands were usually found at the proximal end of the forearm.

Class 4. Band immobile but surrounded by a wound which was not healed. Class 4 status differed from Class 3 status only in that the wound was not healed and there was inflammation, swelling and/or suppuration.

Class 1 status was observed on 295 occasions (66% of the occasions on which band-status was recorded). Class 2 status was observed on 47 occasions (11%). On 41 (87%) of these occasions, the chafing associated with Class 2 status was trivial but, on three occasions, a lump was observed at the distal end of the forearm and, on another three occasions, chafing had caused slight suppuration. Class 3 status was observed on 51 occasions (11%). In some cases, the band had punctured the wing membrane (but this did not always result in the band becoming immobile). On three occasions, the band was barely immobile and was easily dislodged and made free; these bands were still free two weeks later. Class 4 status was observed on 47 occasions (11%). Although this condition looked painful we did not observe bats attending their wounds or seeming to notice them. No other injuries attributable to the bands were observed.

Table 1. The number of individuals of *Pipistrellus nanus* recaptured at selected intervals after banding. See text for definition of Classes. Percentages are given in brackets

Weeks after banding	Sample size	Class 1	Class 2	Class 3	Class 4
2–3 weeks	50	32 (64%)	3 (6%)	4 (8%)	11 (22%)
6–7 weeks	31	23 (74%)	4 (13%)	1 (3%)	3 (10%)
10–11 weeks	10	8 (80%)	2 (20%)	0 (0%)	0 (0%)
18–19 weeks	26	23 (88%)	1 (4%)	1 (4%)	1 (4%)
20–21 weeks	19	13 (68%)	1 (5%)	4(21%)	1 (5%)
30–31 weeks	23	15 (65%)	1 (4%)	4 (17%)	3(13%)
39–39 weeks	20	11 (55%)	3 (15%)	6 (30%)	0 (0%)

Changes in band-status during the study

Cross-sectional analysis of band-status at selected intervals after banding indicated that the percentage of bats in each class changed with time after banding (Tab. 1). The percentage in Class 1 (no injuries) increased steadily from 2–19 weeks and then decreased steadily. Although this trend was matched by the concomitant decrease, and then increase, in bats with some degree of injury (Classes 2–4) during weeks 2–19, the changes within each of these classes were erratic. Table 1 also shows that, irrespective of the time after banding, the majority of bats had free bands (Classes 1 and 2), and, from week 20 onwards, the percentage with free bands remained almost constant (69–73%).

Longitudinal analysis shows how the band-status changes with time for individual bats. The data for 25 bats from Cohort 1 which were recaptured at least nine times and were still members of the Kapalasa population in Period 3 were analysed in this way. The number of recaptures ranged from 9–15 (mean 11.5 ± 1.9). For 12 of these bats (48%), the band-status was invariably Class 1 and these bats appear to have been trouble-free throughout the study. The remaining 13 bats had injuries ranging from Class 2 to Class 4, which lasted from no more than two weeks to as long as 40 weeks. The records of band-status for five individuals are given in table 2 to illustrate a range of scenarios. Male 55 was typical of the 12 bats which were trouble-free. Male 46 was one of two bats for which band-immobility was observed only once. Female 60 was one of four bats which exemplified two separate incidences of band-immobility. Male 41 was one of four bats with intermittent periods of comparatively short-lasting band-immobility. Female 18 had the worst record and was one of three bats with periods of long-lasting band-immobility.

The band-status of an individual bat could remain the same, or it could change from one class to any other class, within the two-week interval between consecutive censuses (Tab. 2). Of particular interest, however, are the changes – and lack of changes – from band-free status to band-immobile status, and vice-versa. Therefore, we analysed every pair of consecutive recaptures (n = 293) for 65 bats which were caught during consecutive censuses. The possibilities, and their frequencies of occurrence, were: band-free to band-free 70%; band-free to band-immobile 11%; band immobile to band-free 8%; band-immobile to band-immobile 11%. It is evident that free bands tend to stay free, and that immobile bands, almost as often as not, become free. It is relevant, also, that 42 (56%) of the 75 bats which were recaptured were never observed with an immobile band and that, for the 33 bats which were observed with immobile bands at sometime during the study, the number of times that the band was observed to change from free to immobile ranged from 1–4.

Table 2. Records of band status for five bats which illustrate different scenarios, selected from the records of 25 bats from Cohort 1 which were recaptured at least nine times. M = males, F = female. B = census when the bat was banded. – = censuses when the bat was not captured. See text for definition of band status Classes. The band was free in Classes 1 and 2, but immobile in Classes 3 and 4. Bats M41 and F18 were banded by Technique A; bats M55, M46, and F60 were banded by Technique B (details in text).

Bat	Census at which band status was recorded																		% times band immobile	Number of bats with similar records
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
M55		B	–	–	1	–	1	1	1	1	1	1	1	1	1	1	1	1	0	12
M46		B	1	–	–	1	–	1	–	4	1	1	1	1	–	2	1	1	9	2
F60		B	1	1	1	4	–	1	1	–	1	1	1	1	4	–	3	1	17	4
M41		B	3	4	1	2	1	2	4	2	3	3	3	1	3	3	–	3	60	4
F18	B	4	4	4	3	–	3	3	3	3	3	3	3	3	4	2	2	3	87	3

The records of band-status for each of the 25 bats from Cohort 1 which were recaptured at least nine times showed that bands were free for 13–100% of the occasions when the bats were recaptured. The numbers of occasions when the band was free were categorised as <25%, 26–50%, 51–75%, and 76–100% of the occasions when the bat was recaptured. The number of bats in each category was 2 (8%), 1 (4%), 5 (20%) and 17 (68%) respectively, and 12 (48%) were trouble-free (Class 1) on all occasions. For 48 bats recaptured 1–8 times, the results were similar: the percentages were 6%, 15%, 10% and 69% respectively, and 63% of these bats were trouble-free on all occasions.

These data, collectively, show that band-status may change frequently. However, the majority of bats were trouble-free on most occasions, and those which had some form of injury on one occasion were likely to show an improvement by the next occasion.

Band-status in relation to banding technique

We compared the severity, onset and duration of injuries observed in bats banded by Techniques A and B. To eliminate variables, such as differences in the age of the bats and the effects of the seasons, we used data from Cohort 1 only. Technique A was more harmful than Technique B: bats banded by Technique A were more prone to injuries and their injuries tended to develop sooner, last longer and be more severe (Tab. 3). The longitudinal records of two bats banded by Technique A (F18 and M41) and three bats by Technique B (M46, M55, and F60) are given in table 2.

Did the banding technique influence the number of times a bat was recaptured? Bats banded during Census 1 (Technique A) were compared with bats banded during Census 2 (Technique B) and, to standardise the maximum number of recaptures possible, we counted recaptures from Census 3 onwards (excluding Census 6 which was incomplete) for both groups. For bats banded by Technique A, the number of recaptures ranged from 0–15 (mean 5.8 ± 4.7, $n = 40$); for Technique B, the number of recaptures ranged from 0–13 (mean 4.7 ± 4.7, $n = 21$). There was no significant difference (Mann-Whitney $U° = 448.5$, $p = 0.66$). Thus the banding technique did not affect the number of times that any bat was recaptured.

Did banding technique influence the number of bats which were "lost" from the Kapalasa population? A bat was considered to be lost from the Kapalasa plantation during Period 1 if it was not recaptured subsequently, or lost during Period 2 if it was not recaptured during any of the four censuses conducted in Period 3. Forty bats (from Cohort 1) were banded by Technique A and, of these, 24 (60%) were lost during Periods 1 or 2. Similarly, forty-four bats (also from Cohort 1) were banded by Technique B and, of these, 23 (52%) were lost. Therefore the number of bats lost from the population was not af-

Table 3. The prevalence, severity, onset and duration of injuries in bats banded by Techniques A and B (described in Methods). To eliminate effects of age and season, all data are from Cohort 1. Free bands = Classes 1 and 2; immobile bands = Classes 3 and 4.

	Banding Technique A	Banding Technique B
Prevalence and severity of injuries		
Total number of bats banded and recaptured	31	33
Percentage of bats which experienced some band-immobility	61	33
Total number of recaptures	193	211
Percentage of times each class of band status was observed:		
Class 1 (no injuries)	50	81
Class 2	14	6
Class 3	20	7
Class 4 (severest injuries)	16	6
Onset of injuries		
Number of bats observed 2–5 weeks after banding	21	25
Percentage with immobile bands 2–5 weeks after banding	67	24
Duration of injuries		
Number of bats recaptured 9–15 times	10	15
Percentage which were entirely trouble-free (Class 1 only)	30	60
Percentage with Class 4 observed at least once	70	40
Percentage with free bands on:		
more than 75% of occasions	40	87
less than 25% of occasions	20	0

fected by banding technique ($\chi^2 = 0.46$, $p = 0.5$). Further information about losses of bats from the population is given below.

Band-status in relation to time after banding

To analyse how band-status may have changed with time after banding, we used the calendar of catches which was laid out according to the number of weeks (in two-week intervals) after the bat was banded. For every interval after banding, we calculated the percentage of bats which had immobile bands: data from all recaptured bats (n = 75) were used. A pattern was evident (Tab. 4). Injuries severe enough to immobilise the bands (classes 3 and 4) often developed very soon after banding with the result that 30% of the bats had immobile bands after 2–3 weeks and 24% had immobile bands after 4–5 weeks. Subsequently, the percentages with immobile bands dropped very markedly during weeks 6–19, but then increased during weeks 20–29 and then increased again during weeks 30–41. This pattern was more conspicuous for the bats banded by Technique A than for those banded by Technique B – mainly because more of the bats banded by Technique A experienced band-immobility, and the first period of immobility occurred earlier (see Tab. 3).

To ascertain why the percentage of bats with immobile bands decreased during weeks 6–19 after banding, we examined the longitudinal records for each bat which was observed during weeks 2–5 and also during weeks 6–19 (n = 42 bats). Sixty-six percent of these bats remained band-free, two percent remained band-immobile but 32% changed from being band-immobile to band-free. A similar analysis showed why the percentage of bats with immobile bands increased after week 20: 34% changed from being band-free (prior to week 20) to band-immobile whereas only 3% changed from band-immobile to band-free (59% remained band-free and 3% remained band-immobile). We cannot explain why band-immobility decreased 6–19 weeks after banding, or why it subsequently increased.

Table 4. The percentages of recaptured bats with immobile bands (Classes 3 and 4) in relation to time (in two-week intervals) after the bats were banded.

Time after banding (weeks)	Two-week intervals	Number of intervals	Mean number of bats observed in each interval	% bats with immobile bands	
				Mean	Range
2–5	2–3 and 4–5	2	45.5	27.0	24–30
6–19	6–7 to 18–19	7	17.6	5.0	0–13
20–29	20–21 to 28–29	5	22.4	24.8	17–35
30–41	30–31 to 40–41	6	19.3	32.5	28–42

Band-status in relation to climatic conditions

Malawi has three seasons: a hot wet season from November to early April, a cool dry season from April to July and a hot dry season from August to October. Climatic averages for Zomba (20 km from Kapalasa Farm) are given by Happold and Happold (1990). To investigate changes in band-status in relation to season, we calculated the percentage of bats observed with immobile bands during each of four consecutive censuses in each season (Tab. 5). We also recorded the number of rainy days, total rainfall, mean daily minimum temperatures, and mean daily maximum temperatures for every day between the first and last of the four consecutive censuses in each season (Tab. 5). There was no significant difference in the percentages of bats with immobile bands from season to season (Kruskal-Wallis $H_c = 0.203$, $\chi^2_{0.05,2} = 5.99$, $p = 0.9$) although there were marked changes in rainfall and temperature.

We also tabulated the worst band-status recorded during each season for bats which were recaptured at least once during each season, and then noted the frequencies with which the band-status improved, deteriorated or stayed the same from one season to the next season. For the transition from the hot dry season to the hot wet season, 8 improved, 4 deteriorated, and 10 remained the same. For the transition from the hot wet to the cool dry season, 6 improved, 7 deteriorated, and 11 remained the same. There was no differ-

Table 5. Band status in relation to climatic conditions recorded at Kapalasa Farm from Census 2 to Census 5 (hot dry season), Census 7 to Census 10 (hot wet season) and from Census 15 to Census 18 (cool dry season).

	Season		
	Hot dry	Hot wet	Cool Dry
Number of rainy days	3	29	2
Rainfall (mm)	4	445	9
Minimum temperature °C:			
Mean ± SD	17.9 ± 2.5	19.6 ± 1.9	14.2 ± 2.4
Range	13–22	17–24	10–22
Maximum temperature °C:			
Mean ± SD	29.4 ± 3.2	27.9 ± 1.8	24.6 ± 2.9
Range	22–33	24–33	16–30
Number of bats observed each census	21–36	18–25	20–28
Percentage bats with immobile bands:			
Mean	25.0	22.3	28.5
Range	8–38	6–37	25–31

ence between the transitions ($\chi^2 = 2.04$, $p = 0.36$) and this is further evidence that band-status was not affected by the seasons.

Band-status in relation to sex

To investigate whether the severity and duration of injuries differed between males and females, we compared the percentage of occasions for which the band was observed to be free for 16 males, and for nine females, which were recaptured at least nine times. The percentages ranged from 22–100% (mean 82.3 ± 26.5) for males, and from 13–100% (mean 73.6 ± 28.3) for females. There was no significant difference between the sexes (Mann-Whitney U° = 87.5, $p = 0.35$).

Responses of the bats

Responses of bats to their bands

Banded bats were observed when they were returned to holding bags after banding, and while they were resting (on the bags or on our hands) prior to being released. We did not observe any bat biting its band or attending to an injury. There was no evidence that the bats chewed their bands at any other time – none of the bands had tooth marks and the band number was always readable although, on a few occasions, cell debris and dried fluids had to be removed from the surface of the band.

Effects of bands on flight and foraging behaviour

Banded bats were usually released at dusk, on the day of the census, before other bats had emerged from their domiciles. The bats were often torpid, and torpid individuals were allowed to warm themselves in our hands or on our arms until they were ready to fly. The banded bats took off strongly and usually spent at least ten minutes flying nearby. During this time, they foraged for flying insects (feeding buzzes were recorded), flew very close to the observers while other unreleased bats were warming up and echolocating, and flew down to a swimming pool (about 4 m diameter) to drink and/or forage. We observed no abnormalities of flight and could not distinguish the flight of the banded bats from that of banana bats which were not banded.

Effects of bands and/or banding on the mass of the bats

During Census 2, we compared the masses of unbanded bats (2.5–3.5 g, n = 22) with those of bats which were recaptured after carrying bands for two weeks (2.5–3.5 g, n = 21). There was no significant difference between the banded and unbanded bats (Mann-Whitney U° = 269.5, $p = 0.3$). Similarly, there was no significant difference between the masses of the banded females (n = 14) and the unbanded females (n = 10) (Mann-Whitney U° = 73.0, $p = 0.85$). During Census 3, we compared the masses of unbanded bats (n = 13) with those of bats which were recaptured after carrying bands for two weeks (n = 11) and for four weeks (n = 24). By this time, the females (all in the early stages of pregnancy) were heavier than the males so the comparisons were restricted to bats of the same sex. Again, there was no significant difference between the masses of the bats in each category (for males, Kruskal-Wallis Hc = 2.67, $\chi^2_{0.5,2} = 5.99$, $p = 0.26$; for females, Kruskal-Wallis Hc = 0.85, $\chi^2_{0.05,2} = 5.99$, $p = 0.65$).

Effects of the bands and banding on "survival" in the Kapalasa population

For this investigation, bats were considered to have been lost if they were not recaptured in the Kapalasa plantation after being missing for four or more consecutive censuses. To investigate whether the loss of bats was related to band-immobility (Class 3 and Class 4), we compared the longitudinal records of bats from Cohort 1 which were lost (after being recaptured 3–5 times, n = 11) with those which were not lost (after being re-

captured at least nine times, n = 25). The records for the lost bats were marginally better than those of the bats which were not lost. For example, for the lost bats, the percentage of occasions on which the band was immobile ranged from 0–50% (cf. 0–87% for bats which were not lost); and only 9% of the lost bats had immobile bands on more than half the occasions when recaptured (cf. 16% for bats which were not lost). Furthermore, bat F18 which had the worst record of band-immobility (Tab. 2) was not lost.

Further evidence that band-immobility was unlikely to cause the loss of bats was obtained by analysing the status, when last observed, of all bats in Cohort 1 which were lost (n = 42). Only 4% of these bats had immobile bands, whereas 96% had free bands (Class 1 79%, Class 2 18%).

Although these data suggest that losses are not related to band-immobility, it is possible that some bands may have caused injuries more severe than any which were observed, and that these resulted in the death of the bat. However, while examining furled leaves at Kapalasa, we never found a dead or unfit banded bat. It is also relevant that (a) at other localities, we recaptured three bats which had been lost from the Kapalasa population, and (b) six bats which appeared to have been lost, turned up again after being missing for 24 to 34 weeks.

Losses of bats caused by the procedures of banding and/or censusing were impossible to assess in this study. Losses of male bats from Cohort 1 in Period 1 were very low: 30 were banded, and of these four were never recaptured, four were lost at the beginning of Period 2, and 22 were still being recaptured during Period 3. Evidently banding did not disturb the majority of the males enough to make them permanently abandon the plantation for the duration of the study, even though other roosts were available and were utilised some of the time. The number of times these males were recaptured was high (mean 7.2 ± 4.5), which also suggests that they were not particularly distressed by the censuses. Losses of females (all pregnant) during Period 1 were much greater than the losses of males: 54 were banded, and of these 16 were not recaptured and six others were lost. The females were recaptured less often (mean 3.6 ± 4.5) than the males. The disproportionate loss of females was not a result of females being affected more adversely by the bands because the sexes were affected equally. Possibly the females were more distressed by the banding and the censuses, and responded by abandoning the Kapalasa plantation, but there could be alternative explanations for the disproportionate loss of females (e.g. the occurrence of pregnancy-related mortalities and/or higher predation due to the clumping of females at roosts).

Effects of the bands and/or banding on social behaviour

Throughout most of the year, including during Period 3 when mating begins, male banana bats sometimes roost singly and sometimes in labile groups composed of one (rarely two) males and 1–10 females. During the time of parturition and lactation, females very rarely roost with adult males, but at all other times of the year they usually roost with males and, during Period 3, they almost always roost with males (Happold and Happold 1990, 1997). We were able to compare two aspects of the roosting behaviour of banded bats with that of bats which were not banded; Period 3 was chosen for the comparison because this was the time when male-female relationships were particularly important.

Firstly, we compared the roosting behaviour of females which were banded and not banded. During Period 3, 20 banded females were recaptured 1–4 times, resulting in 50 observations of banded females at their roosts. On all but two occasions, these females were roosting with males, and the band-status of the two females which were found roosting without a male (on one occasion each) was Class 1. Band-immobility was observed on 17 (34%) of the 50 occasions. During the same period, 29 females which were not banded were captured, with their roost associates, at localities other than the Kapalasa plantation. On all but three occasions, these females were found with males. These data indicate that

the roosting behaviour of females was not adversely affected by censusing, banding or by the status of the bands.

Secondly, we compared the roosting behaviour of males which were banded and not banded. During Period 3, 27 banded males were recaptured 1–4 times resulting in 86 observations of banded males at their roosts. Banded males were found with females on 45% of occasions. During the same period, 23 unbanded males were observed and, of these, 69% were found with females. These data suggest that banded males were found less often with females, but we have no evidence that this was disadvantageous.

Discussion

In recent years, there has been a rapid increase in the number and scope of studies involving bats, and a growing need for bats to be recognisable either as individuals or as members of a particular group. For example, our investigations of the reproductive biology, population dynamics and social behaviour of the banana bat, *Pipistrellus nanus*, could not have been carried out successfully unless the identity of each individual in the Kapalasa population was known. At the beginning of the study, we were inexperienced and we did not know if the bands and/or banding procedures would harm or distress the bats. Before commencing the study, we sought advice from other bat-banders (which was conflicting) and from the literature (which was hard to find and obtain). There is clearly a need for bat-banding information to be accumulated and published in well-known, accessible sources.

During this study, we were able to obtain information about the effects of bands and frequent censusing because banana bats had a high level of fidelity to particularly clumps of bananas in the plantation, and consequently we were able to recapture banded bats many times (Happold and Happold 1996). We were able to follow band-status in the population as a whole, and in individuals who were recaptured at two-week intervals for the best part of a year. Our classes of band-status are very similar to those defined and described by Dwyer (1965) and currently used for bats by the Australian Bird and Bat Banding Scheme. It is possible (and for some species highly probably) that bands also cause some injuries which are fatal, but these are very rarely observed. For the banana bats, survival in the banded population was high, particularly for males and particularly during times of the year when there was neither courtship, immigration or emigration. We obtained no evidence that losses of bats from the population were the result of band-caused mortality, although some bats (particularly pregnant females) might have abandoned their roosts in the Kapalasa plantation because they were distressed by being captured and/or banded. Some banded bats which no longer roosted in the plantation were recaptured elsewhere, proving that at least some losses were not mortalities. Losses did not appear to be related to the band-status of the bats when they were last observed. Band-status did not change as a result of seasonal changes in rainfall and temperature, nor was it related to sex. Most bats remained free of injury for most or all of the time, but injuries could arise unpredictably and also heal themselves unpredictably. Banding did not result in weight-loss, and did not affect the behaviour of the bats to the extent that reproductive processes (such as females rearing their young, and roosting with males during the mating season) were compromised. Consequently, the banding of these bats enabled us to complete our research with satisfactory results.

To what extent does this help other bat-banders to design projects on other species, and interpret the results? At the moment, it is not possible to answer this with certainty, and this again highlights the need for more information so that widespread comparisons can be made. *Pipistrellus nanus* belongs to a cosmopolitan group of genera of small vespertilionids collectively known as the pipistrelles and serotines. There are approximately

50 pipistrelles in the genus *Pipistrellus*, 33 species of serotines in the genus *Eptesicus* and additional species in other closely related genera (Koopman 1993). All are of similar size or a little larger than *Pipistrellus nanus* and, like *Pipistrellus nanus*, they all have a comparatively narrow propatagium. Furthermore, none of these bats are restless or free-hanging at their roosts and therefore their bands are unlikely to chafe them, or fall over their wrists, during roosting. Provided that these species do not damage their bands by chewing them, the physical effects of the bands are likely to be similar to those of *Pipistrellus nanus*. However, they may respond differently to being disturbed, handled, banded, and recaptured. For example, banana bats do not hibernate but bats which do hibernate can be very seriously disadvantaged if they are disturbed at their hibernacula (Jones 1976; Keen and Hitchcock 1980; Tuttle 1979; all in Barclay and Bell 1988). Another consideration is that banana bats are very common throughout most of Africa, and the banding of one small population was not going to compromise the survival of the species. In contrast, even if all other factors appeared to be similar, the banding of rare pipistrelles and serotines should not be justified solely on the basis that banding with flanged bands proved almost harmless to banana bats.

It is probable that many species of pipistrelles, serotines, and other small vespertilionids can be banded with consequences similar to those described in this study, and therefore banding projects on these species can be planned, and the results interpreted, with reasonable confidence. However, extrapolating from banana bats to larger vespertilionids and to species in other families is probably not justified. For example, some species often damage metal bands by chewing them and, as a result, the edges may become jagged and inflict severe injuries, the band may become crushed so it no longer moves, and the writing on the band may become illegible (Barclay and Bell 1988; Bonaccorso and Smythe 1972; Cranbrook and Barrett 1965; Dwyer 1965; Hitchcock 1957). Similarly, species which have a wide propatagium (e.g. pteropodids, rhinolophids, mormoopids, and phyllostomids) cannot be banded satisfactorily on their wings unless the propatagium is punctured to create a hole to accommodate the band (Barclay and Bell 1988), and Jolly (1988) found that this technique was also superior in the case of the emballonurid *Taphozous georgianus*. Furthermore, some species (e.g. rhinolophids) spend a lot of time hanging upside-down, swivelling from side to side and quivering as they echolocate, and it has been suggested that this may increase the likelihood of the band sliding down the forearm and onto the wrist (Dwyer 1965).

It has been demonstrated that small birds and bats are not seriously disadvantaged unless they carry devices (such as transmitters) which weigh more than 5% of the body weight (Barclay and Bell 1988). Banana bats are particularly small and delicate, but because the mass of each band was only 1.5% of the mass of the lightest individuals (2.5 g), and 1.2% of the mean mass of average individuals (3.2 g), they are unlikely to have been disadvantaged by the mass of the band. Furthermore, female banana bats adjust to changes in mass amounting to as much as 80–90% of the mean mass of the species when they are carrying two foetuses (combined mass 2.5 g at full term), or when transporting non-volant young (individual mass 1–3 g) from one roost to another. In this study, banded females survived pregnancy and lactation without showing any evidence of being less fit than unbanded females.

Some bat banders believe that injuries are caused by careless banding while others believe that many injuries are caused by bats biting their bands (Greenhall and Paradiso 1968). The banana bats did not bite their bands, but some individuals were injured by their bands and the prevalence and severity of the injuries was affected by banding technique in a way which shows that careless banding can indeed result in more injuries. In our case, we were not careless but, at first, we were inexperienced and the outcome was the same – bats banded by our first technique (Technique A) suffered more injuries which developed sooner, became more serious and lasted longer than bats banded by our

second technique (Technique B). Consequently, we can make two recommendations: (1) flanged metal bands should be fitted as loosely as possible, and (2) new bat-banders should receive training from experienced banders before attempting to work on their own. Bat banding is not as easy as it appears to be.

As information accumulates, it will become increasingly easier to make wise, ethical decisions about which species are safe to band and which investigations are important enough to justify banding. We felt, and still feel, that the information we obtained about the reproduction, population dynamics and social behaviour of the banana bats at Kapalasa justified banding them. We showed that banana bats exhibit roost fidelity despite the ephemeral nature of their roosts, that group membership is highly labile, that multiple matings over a period of 2.5 months are possible, and that there is potential for sperm competition (Bernard et al. 1997; Happold and Happold 1996). We harmed very few individuals, did nothing to jeopardise the survival of the species and, at the end of the study, we removed the bands from as many bats as possible. From our point of view, the banding was justified.

The bats themselves may have a different opinion. We received a letter recently from Malawian friends who are employed on Kapalasa Farm. As a result of our work, they learned a lot about banana bats and wrote, very sensitively, about them: "The bats nowadays are many. Bats are now rejoicing in the new plantations simply because they are missing some-one who can catch them."

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Zusammenfassung

Auswirkungen von Fledermausklammern und Markierung auf eine Population von Pipistrellus nanus (Chiroptera: Vespertilionidae) in Malawi

Die Arbeit enthält Informationen über den Effekt von Metallklammern und über die Verfahren, die mit Beringung und häufiger Kontrolle verbunden sind, auf eine Population von *Pipistrellus nanus*, einer sehr kleinen Glattnase. Die Tiere wurden über 10 Monate in Intervallen von etwa 2 Wochen an ihren Quartieren in einer Bananenplantage kontrolliert; 120 Bananenfledermäuse wurden markiert und 75 mehrfach wiedergefangen (447 Wiederfänge). Die besten Daten lieferten 64 Adulte (während der ersten 6 Kontrollen beringt), von denen 25 mehrfach (9–15mal) wiedergefangen wurden. Der Effekt der Metallklammern auf die Fledermäuse wurde bei jeder Kontrolle festgehalten. Wir unterschieden 4 Zustandsklassen von 1 (Klammer frei beweglich ohne Verletzung, in 66% aller Fälle beobachtet) bis 4 (Klammer unbeweglich mit offener Wunde, in 11% aller Fälle beobachtet). Die Ergebnisse zeigen, daß (a) die meisten Fledermäuse der Klasse 1 angehörten, einige aber Verletzungen aufwiesen (Klassen 2–4), die sich oft unvorhersagbar verschlimmerten; (b) der Zustand sich ohne erkennbares Muster mit zunehmender Zeit nach der Markierung veränderte; (c) der Zustand nicht vom Klima noch vom Geschlecht abhängig war; (d) die Markierung nicht Flug- und Jagdverhalten, Körpermasse oder Überlebensdauer in der Population beeinflußte; und (e) das Quartierverhalten unverändert war. Fledermäuse, die von uns ohne Erfahrung während der ersten Kontrolle markiert wurden, trugen ein größeres Verlet-

zungsrisiko als Tiere, die später markiert wurden, nachdem wir unsere Technik verbessert hatten. Mit Hilfe der Beringungsmethode konnten wir das Sozial- und Fortpflanzungsverhalten dieser Art studieren und glauben, daß die dabei erzielten Resultate die Markierung einer kleinen Population dieser häufigen und weitverbreiteten Art rechtfertigten. Wir vermuten, daß andere Arten kleiner Glattnasen in ähnlicher Weise auf Metallklammern reagieren werden, aber eine Ausweitung auf Arten anderer Familien ist wahrscheinlich nicht möglich. Wir empfehlen, daß Metallklammern so locker wie möglich angelegt werden, daß Anfänger von erfahrenen Beringern ausgebildet werden sollten, und daß die Beringung von Fledermäusen nur gestattet werden sollte, wenn sehr gute wissenschaftliche Gründe dafür vorliegen, und wenn ein Schaden für Individuen und Populationen von Fledermäusen unwahrscheinlich ist.

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The diet of the Noctule bat *Nyctalus noctula* in Latvia

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Abstract

As indicated by the diet, noctule bats in an agricultural landscape in Latvia feed mostly near or over water; catching predominantly larger non-tympanate insects such as Trichoptera, Ephemeroptera, Coleoptera, and Hemiptera and also Lepidoptera, Neuroptera, and Diptera in smaller numbers. The diet reflects limitations on the echolocation call system and flight characteristics of this large, fast-flying bat. The smallest insects in the diet (ca. 9 mm wingspan) conform in size with what is theoretically predicted, although they are taken in rather small amounts. Therefore, the minimum prey size is probably set by perceptual constraints.

Key words: Chiroptera, echolocation, insects, predation

Introduction

The common noctule (*Nyctalus noctula* Schreber, 1774) is a large (30 g) aerial-hawking insectivorous bat common throughout most of Europe, ranging northward to about 60° N in Scandinavia. Being relatively large with high wing loading (Norberg and Rayner 1987), this bat would be expected to feed on mostly large prey; because it flies fast and uses low frequency (18–26 kHz; Zbinden 1989) echolocation calls to increase the detection range. This would suggest that it probably cannot prey on insects as small as most nematoceran dipterans, which can only be detected over very short distances (Barclay and Brigham 1991).

Previous observations suggest that the noctule specialises on very large insects such as crickets and large scarabaeid beetles (Poulton 1929; Cranbrook and Barrett 1965). However, more recent investigations of this and closely related species indicate that they also feed on small insects such as chironomids (Jones 1995; McKenzie and Oxford 1995; Waters et al. 1995). Thus, the latter observations challenge the earlier reports. It is also possible that the fauna of larger insects were impoverished in urban and intensively farmed areas of southern England where the latter studies were conducted, and that the bats may have responded to nontypical situations prevailing over farm ditches and around street lights.

Other recent studies in continental Europe suggest that the noctule preferentially forages over water, when available, and near street lamps (Kronwitter 1988; Rachwald 1993), feeding mostly on relatively large insects such as mayflies, caddis flies and moths (Gloor et al. 1994; Beck 1995). The purpose of the present study was to investigate the diet of the common noctule in two farmland areas of Latvia, each with high habitat diver-

sity, including several lakes and rivers, and where street lamps are few. This study is the first to investigate the diet of bats in the Baltic area.

Material and methods

Faeces were collected in tree roosts used by colonies of noctules in a small-scale farming landscape (pasture, arable fields, and coniferous and mixed woodlands) of eastern Latvia. The first sample was obtained from a woodpecker hole in a pine (*Pinus silvestris*) in Rucava Village, 10 km east of Lake Pape (56°11′ N, 21°03′ E) in September 1992. The second sample came from a hollow lime tree (*Tilia cordata*) at Janopole, 7 km SSE of Rezekne (56°28′ N, 27°23′ E). In this case, the droppings were collected in June 1995, while bats occupied the roost. The two roosting holes were both situated about 5 m above the ground and within flight distance of lakes and rivers, which we judged to be suitable for foraging. The first roost was located near lake Pape and 4–5 km from the Sventaja River. The second roost was located within 10 km of several small lakes and ponds and about 12 km from Lake Raznas.

The faecal pellets were kept frozen until they were analysed. The droppings were soaked in a mixture of water and ethanol for a few minutes and then teased apart using needles and pointed tweezers under a Wild M5 binocular (dissecting) microscope at 12-40 X magnification. The prey remains were identified according to order ar family by using various field guides (e.g. Chinery 1986; McAney et al. 1991) and a collection of whole insects. The proportions (by volume) of each prey category were estimated for each dropping separately, and the percentages were then averaged. Due to the many potential biases involved in this method (Kunz and Whitaker 1983; Robinson and Stebbings 1993), the percentages should only be regarded as a rough estimate of the dietary composition. We also include the frequency of occurrence of each prey category (the percentage af the faecal pellets in which the category was found). This measure may be less biased, but on the other hand gives almost no indication of the relative importance of the various prey categories. Since it does not add to 100%, it is virtually useless for statistical (comparative) purposes (Whitaker 1988).

Results

Both samples consisted almost entirely of insects that normally occur near water, suggesting that the bats mostly foraged over lakes and ponds, several of which occurred in the vicinity of the roosts. The first faecal sample (from Rusava) was dominated by beetles (Coleoptera), mainly or exclusively medium-sized water beetles (family Hydrophilidae) and diving beetles (Dytiscidae), together representing 64% of the sample by volume (Tab. 1). The second most important prey category was caddis flies (Trichoptera), mostly af the family Limnephilidae. Moths (Lepidoptera), mayflies (Ephemeroptera), small flies (Di-

Table 1. Recovered remains (%) of arthropod taxa from droppings of *Nyctalus noctula* collected in two tree holes in Latvia. One hundred droppings were analysed from each of the two localities.

Prey category	Locality 1		Locality 2	
	% volume	% frequency	% volume	% frequency
Trichoptera	24	39	36	60
Coleoptera	64	62	2	10
Lepidoptera	4	7	13	28
Ephemeroptera	4	7	13	31
Hemiptera	3	4	15	29
Neuroptera	0	0	9	15
Diptera	2	5	7	16
Siphonaptera	0	0	0	1
Acarina	0	3	0	1

ptera, mostly Chironomidae) and water bugs (Hemiptera; Heteroptera) were also obtained from this sample, but only in small amounts (2–4% each). Among the water bugs, members of the family Corixidae were the most frequent. Three of the faecal pellets included parasitic mites (Acarina), which probably were ingested inside the roost following grooming of the fur. This may also apply to bed bugs (*Cimex* sp.), which were recovered from one of the droppings.

In the second sample (from Rezekne), the diet was even more diverse, but like the first sample, it consisted almost entirely of insects that normally occur over water. This sample was dominated by caddis flies (Trichoptera, mostly Limnephilidae), comprising 36% of the sample, but also included large amounts of moths (Lepidoptera; 13%), mayflies (Ephemeroptera; 17%), bugs (Hemiptera, including Corixidae; 15%) and brown lacewings (Neuroptera, Hemerobiidae; 9%). Diptera represented only 7% of this sample. One flea (Siphonaptera) must have been ingested during grooming, like the ectoparasites found in the first sample.

To obtain a rough idea of the size of some of the prey items, the length of some wings which were recovered from the faecal samples more or less whole, were measured. Among the caddis flies, the wings (N = 10) were 5–13 mm long, indicating total wingspans of the smallest specimens of just over 1 cm. The mayflies were apparently of similar size, as recovered wings (N = 2) were 5–6 mm long. This also applies to beetles (5 and 10 mm; N = 2). The wings of small flies (Diptera) were 4–6 mm long (N = 6), again indicating wingspans of around 1 cm for the smallest specimens.

Discussion

The diet of the noctule is varied. In England it is dominated by farmland insects, such as *Geotrupes*, *Aphodius*, and *Melolontha* beetles (Coleoptera; Scarabaeidae), crane-flies (Diptera; Tipulidae), dung flies (Diptera; Scatophagidae) and moths (Lepidoptera) (Jones 1995; McKenzie and Oxford 1995). In Germany and Switzerland, caddis flies (Trichoptera), mayflies (Ephemeroptera) and true bugs (Hemiptera; Heteroptera) were also included in the diet, as well as non-biting midges (Diptera; Chironomidae), suggesting that the bats in these cases fed near or over water (Gloor et al. 1994; Beck 1995). The apparent difference in the diet of noctules between England and central Europe may perhaps be related to differences in geology and landscape. In southern England, lakes or large rivers are relatively scarce, while they may form a dominant part of the countryside further east and north on the European mainland, where glaciations have been more prevalent.

Insects that emerge from water surfaces, such as mayflies, caddis flies, and chironomids, are important prey for many aerial-hawking bats in Europe and elsewhere. However, some aquatic insects appear to be more important as bat food than others, for reasons that are not clear. For example, Daubenton's bats *Myotis daubentonii* (Kuhl, 1819) and common pipistrelles *Pipistrellus pipistrellus* (Schreber, 1774), two of the most common species in northern Europe, frequently feed over water (Swift and Racey 1983; Racey and Swift 1985), where they consume large numbers of chironomids but surprisingly few caddis flies, mayflies, and other larger insects (Swift et al. 1985). A very similar situation applies to the northern bat *Eptesicus nilssonii* (Keyserling and Blasius, 1839) and the particoloured bat *Vespertilio murinus* Linné, 1758, which also catches mainly small insects when foraging over water in Scandinavia (Rydell 1986, 1992 a). Likewise, Leisler's bat *Nyctalus leisleri* (Schreber, 1774), feeds mainly on chironomids and yellow dung flies (*Scatophaga* spp.) in England and Ireland (Sullivan et al. 1993; Waters et al. 1995). The noctules caught many more of the larger insects than any of the other species, as might have been expected, but they also caught occasional flies with wingspans of about 1 cm or half a wavelength of the search phase echolocation calls (20 kHz translates to a wave-

length of 22 mm). This minimum prey size corresponds precisely with those recorded by Jones (1995) for noctules in England. It also corresponds with the minimum prey sizes recorded for the other species, in the sense that the smallest prey had wingspans a little less than half a wavelength of their echolocation calls. It is also very similar to the sizes expected based on experiments and theory (Waters et al. 1995), suggesting that the minimum prey size is determined by perceptual constraints rather than by considerations based on optimal foraging (Anthony and Kunz 1977; Barclay and Brigham 1991).

Smaller bats such as the pipistrelles are able to catch large aquatic insects including mayflies and caddis flies, although they catch them only in small numbers (Swift et al. 1985), suggesting that handling large prey is not a problem even for small bats. However, we suspect that the availability of larger insects that occur near water not only are constrained by the hunting and handling technique of the bats and the absolute abundance of the prey but also by the behaviour of the insects. Many mayflies and caddis flies are predominantly diurnal or crepuscular, and may only be available to bats that emerge and start to forage early in the evening. In northern Europe, the noctule is always the first bat to appear, half an hour before the pipistrelle and almost an hour before Daubenton's bat, on average (Jones and Rydell 1994). Hence, the noctule would, therefore, be expected to encounter more crepuscular and diurnal insects than any of the other bat species.

Moths were caught much less frequently by the Latvian noctules than by those in England and central Europe. Most nocturnal moths are tympanate, and may thus be well adapted to avoid high intensity echolocating bats such as noctules (Roeder 1967), although moths seem to be at a relative disadvantage near streetlamps (Rydell 1992 b), where noctules often forage (Kronwitter 1988). It is possible that the difference in moth utilisation between Latvia and most of western Europe reflects the relative scarcity of street lamps in the east.

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Zusammenfassung

Die Nahrung des Abendseglers Nyctalus noctula in Lettland

Die Nahrungsanalyse des Abendseglers aus der Kulturlandschaft Lettlands zeigt an, daß dieser hauptsächlich in der Nähe von Wasser oder an der Wasseroberfläche jagt. Er fängt große Insekten ohne Tympanalorgane, größtenteils Trichoptera, Ephemeroptera, Coleoptera und Hemiptera, in geringer Anzahl aber auch Lepidoptera, Neuroptera und Diptera. Die Nahrung spiegelt die Begrenzung des Echoortungssystemes und der Morphologie der Flügel dieser großen, schnellfliegenden Art wieder. Die kleinsten Insekten in der Nahrung (ca. 9 mm Flügelspannweite) stimmen größenmäßig mit dem überein, was theoretisch detektierbar ist, obwohl so kleine Insekten verhältnismäßig selten gefangen werden. Die angewandten Wellenlängen scheinen die Untergrenze für die Größe der Beute festzulegen.

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Behaviour of Alpine ibex (*Capra ibex ibex*) under the influence of paragliders and other air traffic

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Abstract

In summer 1992 we investigated the influence of paragliders and other air vehicles on the behaviour of male ibexes (*Capra ibex ibex*) in a population of the Swiss prealps. Within a range of 1 200 m ibexes fled more frequently from paragliders than from motorplanes, helicopters, sailplanes, and jetfighters. Neither group size, previous activity nor the relative flight altitude of the aircraft (above or beneath the observed group) was found to have any influence on the reaction. Distance fled after encounters between paragliders and ibex ranged from 30–1 200 m (median 650 m) and the changes in altitude while fleeing from 20–500 m (median 200 m). These two parameters were much smaller when reacting to the other air-based vehicles. The daily walking distances were longer on days with paraglider activity compared with days without paraglider activity. Many escape flights went out of the home range normally used by the observed male ibexes. These strong reactions to paragliders were as yet unknown for ibexes. The conservation implications would be regulation of paragliding in some regions to protect these animals.

Key words: *Capra ibex*, Air traffic, paragliders, behaviour

Introduction

The Alps are increasingly becoming a resort for tourism and modern leisure activities. Especially hang- and paragliding have been booming since the eighties in all regions of the Alps, with an increase in Switzerland from 2 800 active pilots in 1980 to nearly 20 000 in 1991. Paragliders are able to fly and soar at low speed and low ground clearance and pilots can take off from almost any slope limited only by meteorological and topographical conditions. With their light and easy to carry equipment, the pilots are able to fly into new and untouched areas.

Studies in North America show that air traffic may affect free-ranging ungulates. Especially low-flying aircraft can cause particularly intense reactions (Calef et al. 1976; Miller and Gunn 1980; Krausman et. al 1986; Harrington and Veitch 1991). Furthermore changing of home range areas and reduced foraging efficiency were found in bighorn sheep (*Ovis canadensis*; Bleich et al. 1990; Stockwell et al. 1991). Alpine chamois (*Rupicapra rupicapra*) show intense flight reactions to paragliders and often seek shelter in the woods (Schnidrig-Petrig 1994).

The Alpine ibex (*Capra ibex ibex*) is probably the most famous Alpine mammal and in some parts of the Alps well known to tolerate human activities like hikers at close distances. However, little is known about its reaction to air traffic. The reintroduction of this once extinct species represents a true success story for conservation (Stüwe and Niever-

GELT 1991) and the fate of ibex in Switzerland is therefore of concern to nature conservation. Ibexes live above the timber line (NIEVERGELT and ZINGG 1986) and are therefore considered to be particularly confronted with paragliders and other air traffic. If they would react strongly on air traffic and especially paragliding as a new leisure activity, this should be of importance for nature conservation.

The aim of our study was to investigate the behaviour of male ibex towards paragliders, compared to other types of aircrafts like helicopters, motorplanes, sailplanes, and jet-fighters.

Material and methods

Study area and animals

The study area lies within the national game reserve Augstmatthorn (Bernese Oberland, Switzerland). The Augstmatthorn region (top at 2 137 m a. s. l.) is characterized by steep slopes interspersed with rocky cliffs. The vegetation on the lower parts is dominated by subalpine coniferous forest. Due to the historic lowering of the timber line, large species-rich alpine pastures have been opened in the higher parts. The ibexes of the study area spend the summer above the tree line. In summer sexual segregation is distinct and males form groups of irregular composition with a size of up to 50 animals. They usually stay at the highest levels of the mountain and tolerate humans within distances of around 15–20 m. The Augstmatthorn ibexes belong to one of the first reintroduced colonies in Switzerland after their extinction in the last century (estimated size of the present population: about 120 animals).

Within 20 km of the study area there are two air force bases where helicopters, jets, and motorplanes take off and land and within 50 km there are two small civil airports. Paragliders usually soar along the mountain slopes into the study area, but they also take off within the study area itself. Since 1989, when we saw the first paragliders in the area, there was a continuous increase in summer (1992 on nearly 20% of days).

Data collection

Data were collected from July to October 1992. Our observation distance to the animals was about 50 m to avoid possible influence. We focused on the first animals that we found in the morning and noted size and position of the group every 30 min from 7:00 h until 20:00 h. One observer searched the sky for approaching air-based vehicles. The topography of the area allowed a good allaround view; approaching aircraft could be detected at great distance. Aircraft that seemed to come closer than 1 200 m to the animals were followed with a telemeter (Sokkisha 3SD3, length 25 cm). The type of aircraft, its closest approach distance to the animals and its flight altitude (above or beneath the observed group) were noted. The second observer noted the behaviour of the animals (feeding, standing, lying). Then he noted, if the animals fled or not. The flight path was marked on a map (scale 1 : 5 000). A flight was decided to be finished when the animals stopped moving for more than 5 minutes. If the animals went out of sight (e. g. if they disappeared into forests or behind rocks), we measured the distance to the point of the last sight contact. Daily walking distances and changes in altitude (not distinguished between walking up or downhill) of any group were calculated by connecting their half hourly position.

Statistical analysis

Statistical analysis of the data was done with a stepwise logistic regression (The Logistic Procedure) on SAS/STAT (SAS Institute Inc. 1989). The response variable was fleeing or not fleeing after an encounter with an air-based vehicle. The following variables were included (variables with an asterisk are indicator variables to which differences in the response variable refer): The different types of flying objects (paragliders*, motorplanes, jet-fighters, helicopters, sailplanes), the approaching distance (< 500 m*, 500–1 200 m), flight altitude (above* and underneath the observed group), group size (1, 2–6*, > 6 animals), and activity (feeding, lying*, standing). For days with several encounters with air-based vehicles only the first encounter was considered in the analysis.

Results

In encounters with sailplanes, helicopters, jet fighters, and motorplanes the ibexes took flight only occasionally. In contrast, they fled in all encounters with paragliders (Fig. 1). Within the range up to 1 200 m, the difference in the frequency of escape flights from paragliders and other aircraft is highly significant, independent of the distance between air-based vehicles and animals. Neither the flight altitude of the aircraft, nor the activity of the group members before the encounter, nor the group size showed any significant influence (Tab. 1). When cases of escape flights occurred, the reaction was strongest to paragliders with a median of the distance fled (DF) of 650 m (30–1 200 m; n = 13) and a covered difference of altitude (AD) of 200 m (20–500 m). These two parameters were much smaller in the reactions to the other air-based vehicles (sailplanes: DF: 200 m, AD: 50 m, n = 3; helicopters: DF: 20 m, AD: 0 m, n = 5; jet fighters: DF: 20 m, AD: 0 m, n = 1; motorplanes: DF: 20 m, AD: 0 m, n = 3). On days with encounters with paragliders groups of ibex walked significantly further (median 1 600 m) and covered more altitude (475 m) than on days without paragliders (800 m/110 m; Fig. 2). Many escape flights went out of the home range normally used by the observed male ibexes (Fig. 3).

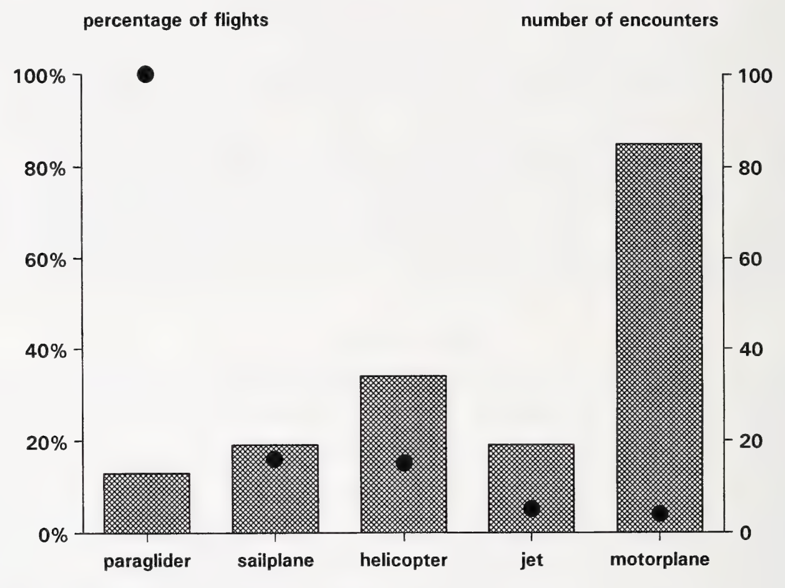


Fig. 1. Percentages of the flights (dots) of male ibexes in encounters with different types of air-based vehicles (columns) within a distance of max. 1 200 m.

Table 1. Results of the SAS Procedure-Logistic (n = 186, Two Response Levels: flight or no flight). Left: p-values of the remaining variables after the Backward-Elimination-Procedure. Right: the order of elimination of other variables with their corresponding p-values. All p-values refer to the corresponding indicator variables (see statistical analysis, *). For the different types of aircraft the indicator variable is paragliders.

Variable	p-value	Variable	p-value
Motorplanes	0.0001	group size: >6 animals	0.609
Helicopters	0.0006	flight underneath	0.531
Jetfighters	0.0006	activity standing	0.505
Sailplanes	0.0127	activity feeding	0.436
distance (500–1 200 m)	0.019	single animal	0.208



Fig. 2. Daily walking distances and changes in altitude during walking of groups of male ibexes on days with and without paragliders (Mann-Whitney U-Test, $p < 0,05$, two-tailed).

Fig. 3. Home range of male ibexes (dotted) and paths fled when paragliders appeared from July to September 1992 on the Augstmatthorn. Thick line: mountain ridge.

Discussion

Paragliders have the greatest influence on the behaviour of male ibex compared with other aircraft. The intense and long flights in this steep terrain which covered altitude differences up to 500 m downhill have never been observed before. It seems that the animals try to escape from the range of the paragliders by seeking refuge in the forest or by changing to the other side of the mountain ridge. Such flights and the increased daily walking distances with the respective changes in altitude result in increased energy expenditure. Hüppop (1995) estimated for a mammal like the ibex (50–100 kg) that one flight could cost up to 2.5% of the daily energy costs (field metabolic rate, distance fled 500 m, altitude difference 100 m). It is likely that the animals are still able to compensate for the energy loss, if these flights occur at low frequency as was observed to date. However, if paragliding should increase and the animals would still flee in the same way, this could have severe consequences on the animals' condition and therefore on their survival in winter.

In the Augstmatthorn region male ibexes show no fear of hikers (flight distances of 15 to 20 m). Furthermore, they have no enemies from the air. It is therefore surprising that they react so strongly to paragliders, but several features make paragliders something special. They fly very slowly and cause almost no flight noise; they can not be heard like engine-powered aircraft when approaching. Their appearance is spatially very variable and the animals have not had much experience with this activity compared to all other aircraft. To date we have no indication that ibexes habituate to paragliders, but on the long run the possibility of habituation is not excluded (for habituation of ungulates to aircrafts: Krausman et al. 1986). Alternatively, it may be that these animals change their normally used habitat, staying close to woods (where they can seek shelter) and avoid exposed sites. If this would happen, it could be a serious problem because the animals would lose the open pastures as feeding sites, an important part of their habitat. Moreover, females with their kids are affected as well. A few observations (females could not be observed as well as males) showed that they react to paragliders as sensitively as males. Long flights and shifts into suboptimal habitats could be critical for kid survival and therefore for the whole ibex population.

In summary, our data show that paragliders are the only air-based vehicles that seem to be a problem for ibexes in our study area. Reports from gamekeepers showed that ibexes in other parts of the Swiss Alps also react strongly to paragliders. It should be worth discussing some regulation of paragliding.

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Zusammenfassung

Zum Verhalten von männlichen Alpensteinböcken (Capra ibex ibex) unter dem Einfluß von Gleitschirmen und anderen Luftfahrzeugen

Im Sommer 1992 untersuchten wir im Gebiet Augstmatthorn (Schweizer Voralpen), wie Gleitschirme und andere Luftfahrzeuge das Verhalten von männlichen Alpensteinböcken (*Capra ibex ibex*) beein-

flussen. Unabhängig von der Distanz zu den Tieren lösten Gleitschirme innerhalb eines Bereichs von 1 200 m häufiger Flucht aus als Segelflugzeuge, Propellermaschinen, Helikopter und Düsenjets. Weder Gruppengröße, vorherige Aktivität der Tiere noch Flugroute (ober- oder unterhalb der beobachteten Gruppe) hatten einen Einfluß auf die Reaktion der Tiere. Die nach Begegnungen mit Gleitschirmen zurückgelegte Fluchtstrecke betrug 30–1 200 m (Median 650 m), die Höhendifferenz 20–500 m (Median 200 m). Viele Fluchten führten weit über das normale Aufenthaltsgebiet hinaus, oftmals bis hinunter zum Wald. Auf andere Luftfahrzeuge reagierten die Steinböcke wesentlich schwächer. An Tagen mit Gleitschirmvorkommen legten sie erheblich längere Wege zurück, die zudem über eine größere Höhendifferenz führten, als an Tagen ohne. Insgesamt reagierten die Steinböcke auf Gleitschirme mit einer kaum erwarteten Heftigkeit. Zum Schutz der Tiere drängt sich in gewissen Gebieten eine Regelung des Gleitschirmfliegens auf.

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A new species of *Oligoryzomys* (Rodentia, Sigmodontinae) from northeastern and central Brazil

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Abstract

A new *Oligoryzomys* species from Central and Northeastern regions of Brazil, *Oligoryzomys stramineus* sp. n., is described based on morphologic, biogeographic, and karyotypic analyses. A comparison with other *Oligoryzomys* species resulted in the distinction of two species groups: one comprising large-sized species with a white ventral surface (*O. chacoensis*, *O. nigripes*, *O. delticola*, and *O. stramineus* sp. n.) and another, comprising small-sized species with a yellow ventral surface (*O. fornesi*, *O. microtis*, and *O. flavescens*).

Key words: *Oligoryzomys stramineus*, new species, distribution, morphology, karyotype

Introduction

The genus *Oligoryzomys* Bangs, 1900 is distributed throughout a large portion of the Neotropical region (Carleton and Musser 1989) and includes species considered to be important components of small mammalian communities in South America (Alho and Pereira 1985; Mares et al. 1981, 1989; Mares and Ernest 1995). However, the taxonomy of this genus is controversial, leading to different taxonomic arrangements that include disparate numbers of species, ranging from 1 (Hershkovitz 1966) to 30 (Tate 1932). Thus, despite extensive studies on *Oligoryzomys* taxonomy (Langguth 1963; Myers and Carleton 1981; Olds and Anderson 1987; Carleton and Musser 1989; Dickerman and Yates 1995) and cytogenetics (Gardner and Patton 1976; Yonenaga et al. 1976; Myers and Carleton 1981; Furtado 1981; Svartman 1989; Sbalqueiro et al. 1991; Espinosa and Reig 1991), this genus is still poorly understood.

Myers and Carleton (1981) and Olds and Anderson (1987) suggested that *Oligoryzomys* comprised two species groups: one, of large-body-sized species, including *O. chacoensis* (Myers and Carlenton, 1981), *O. eliurus* (Wagner, 1845), *O. longicaudatus* (Bennett, 1832), *O. nigripes* (Olfers, 1818), and another, of small-body-sized species, including *O. delicatus* (Allen and Chapman, 1897), *O. flavescens* (Waterhouse, 1837), *O. fornesi* (Massoia, 1973), and *O. microtis* (Allen, 1916).

In this study, we describe a new *Oligoryzomys* species belonging to the large-body-sized group. This species has been morphologically and karyotypically characterized and compared to other *Oligoryzomys* species, especially to those with sympatric and parapatric distributions.

Material and methods

Morphological studies were carried out in 292 specimens of *Oligoryzomys* deposited on the mammals collections of: United States Natural Museum (USNM, Washington, 125 specimens); University of Michigan-Museum of Zoology (UMMZ, Ann Arbor, 12 specimens); Universidade Federal da Paraíba (UFPB, João Pessoa, 65 specimens); Universidade de Brasília (UnB, Brasília, 23 specimens); Museu Nacional do Rio de Janeiro (MN, Rio de Janeiro, 37 specimens), Laboratório de Vertebrados (LV, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 23 specimens). PH (7 specimens) refers to field numbers of P. Hershkovitz and this material will be housed in Museu Nacional do Rio de Janeiro and Field Museum of Natural History (FMNH, Chicago).

The following specimens of *Oligoryzomys* were examined:

O. stramineus sp. n. (45 specimens): BRAZIL: Paraíba State, Pirauá, Natuba (UFPB-AL 2049, 2057, UFPB-LFS 49); Pernambuco State, Angelim (UFPB-G 62) Bom Conselho (UFPB-PMN 360, 497, 561, -G 106) Correntes (UFPB 1863, -PMN 280) Exú (USNM 528416) Macaparana (UFPB-AL 2020); Goiás State, Terezina de Goiás (MN 34439, 46406–35; Minas Gerais State, Montes Claros (LV-FC 10, 21).

O. nigripes (85 specimens): ARGENTINA: Delta del Rio Paraná (MN 24598–99, 245579); BRAZIL: Federal District, Brasília (UnB 295–96, 298–305, 912–13, 962, 999); Espírito Santo State, 24 km SE of Venda Nova (UFPB 1813); Goiás Sate, 30 km E of Flores de Goiás (UFPB 1826, 1828–30, 1832, 1834, 1836–44, 1846–55, 1871, AL 2982); Minas Gerais State, Montes Claros (LV-FC 51) Peirópolis (LV-MW 14) Parque Nacional do Caparaó (PH 10076, 10084, 10107, 10274) Serra do Caparaó (MN 33214, 33218); Paraíba State, Pirauá (UFPB-LFS 49); Pernambuco State, Bom Conselho (UFPB PMN 563) Buique (UFPB 1872); Rio de Janeiro State, Sumidouro (LV-SU 210, 219, 221, 228, 232, 234, CRB 800–03) São Paulo State, Casa Grande (UFPB 1162) Iguape (UFPB 1150, 1152) Taubaté (UFPB 1164). PARAGUAY: Paraguari Department, Sapucai (USNM 121107, 121403–07, 124555–56, 172970) Tacuati 3 km SE of Aca Poi (USNM 293146); Caaguazú Department, Caaguazú (USNM 293144-45); Missiones Department, San Pablo, 20 km of San Ignacio (USNM 390106) San Francisco, 36 km NE San Ignacio (USNM 390107–08).

O. delticola (8 specimens): BRAZIL: Rio Grande do Sul (UFPB 600, 613, 615–17); ARGENTINA: Chacos, Las Palmas (USNM 236285–87).

O. chacoensis (9 specimens): ARGENTINA: Formosa (USNM 236243, 236288–92); BOLIVIA: Entre Rios (USNM 271411–12, 271432).

O. flavescens (57 specimens): ARGENTINA: 25 km SE of Buenos Aires (USNM 331059) General Lavalle (USNM 236274) Concepcion (USNM 259280, 299285, 259290). BRAZIL: Bahia State, Rio Una, 10 km E/SE of São José (UFPB 429); Minas Gerais State, Parque Nacional de Caparaó (PH 10129, 10139, 10422) Viçosa (USNM 541498, LV-LG 71, 72), Rio Grande do Sul State (UFPB 601); São Paulo State, Casa Grande (USNM 461991, 484122–25) Itapetininga (USNM 460516–17, 461049–55, 461990, 461992–94, 484126–33, 484136–37, 405056, 542968–69). PARAGUAY: Caaguazú Department, 24 km NNW Carayaó (UMMZ 133816–17); Canendeyu Department, Curuguaty (UMMZ 124216–17, 124222, 124255) Misiones Department, San Pablo, 20 km W San Ignacio (USNM 390122) Pres. Hayes Department, 24 km NW Villa Hayes (UMMZ 133833, 133841–42). URUGUAY: Maldonado (USNM 259599), Montevideo (USNM 174937) Boca del Arroyo del Tigre, San José (UFPB-AL 922).

O. fornesi (31 specimens): BRAZIL: Federal District, Brasília (UnB 279, 288–91, 965, 294, 931,1212); Goiás State, Corumbá de Goiás (MN 34440) Terezina de Goiás (LV-CRB 674, 708, 709, 733, 747, 757, 768); Paraíba State, Mamanguape (UFPB-MPS 72); Pernambuco State, Buíque (UFPB 1893–94) Bom Conselho (UFPB-PMN 60, 61, 63, 576) Correntes (UFPB 1893–94) Macaparana (UFPB-MPS 34); Sergipe State, 6 km SSL of Matriz de Camaragipe (UFPB 977). PARAGUAI: Caaguazú Department, 24 km NE Carayaó (UMMZ 133818–19) Canendeyu Department, Curuguaty (UMMZ 124218).

O. microtis (57 specimens): BOLIVIA: Beni, Boroica (USNM 460740) Chachuelita (USNM 460739) Chaco Lejo (USNM 391295–97) El Triunfo (USNM 391298) Las Penas (USNM 460741) San Joaquin (USNM 364735, 364738, 364742, 364921, 364923, 391299, 460273, 460742–43) Totai (USNM 364948). BRAZIL: Amazonas State, Terruan, Rio Purus (USNM 461396, 461398–99); Pará State, Belém (USNM 461069–72, 461076, 545290–92) Marabá, Serra do Norte (USNM 543345–46) 75 km N 45 km W Marabá, near Jatobal (USNM 519769, 519771, 521454–62, 521540). PERU: Madre de Dios, Puerto Maldonado (USNM 390112, 390115–19) Rio Manu, 57 km above mouth (USNM 559399–403) Tambopata, 30 km above mouth (USNM 30925) Ucayali, 59 km SW Pucallpa (USNM 499223–25).

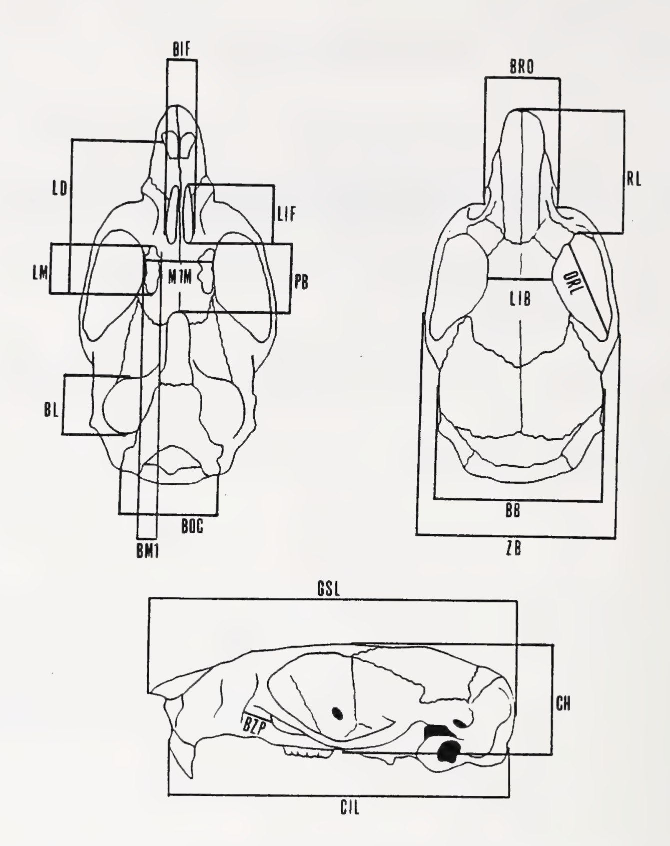


Fig. 1. Ventral, dorsal and lateral view of *Oligoryzomys* skull showing the measurements. The variables abbreviations are in material and methods.

In addition to morphological studies, we karyotyped 62 *Oligoryzomys* specimens: 8 *Oligoryzomys fornesi*, 7 specimens from Terezina de Goiás and 1 from Corumbá de Goiás (Goiás State, Brazil); 5 *O. flavescens*, 3 specimens from Parque Nacional do Caparaó and 2 from Viçosa (Minas Gerais State); 16 *O. nigripes*, 10 specimens from Sumidouro (Rio de Janeiro State), 4 from Parque Nacional de Caparaó, 1 from Peirópolis and 1 from Montes Claros (Minas Gerais State); 33 *O. stramineus* sp. n., 31 specimens from Terezina de Goiás and 2 from Montes Claros. Chromosome preparations followed the procedure of Ford and Hamerton (1956). The skins and skulls of these specimens were deposited in FMNH, LV, and MN collections.

For morphometric comparisons, we took 19 measurements from skulls: Greatest Skull Length (GSL), Condylo-Incisive Length (CIL), Breadth of the Occipital Condyles (BOC), Length of Diastema (LD), Palatal Bridge (PB), Length of Incisive Foramen (LIF), Breadth of Incisive Foramen (BIF), Length of Maxillary Molars (LM), Breadth of First Maxillary Molar (BM1), External Alveolar Breadth (M1M), Bullae Length (BL), Cranial Height (CH), Rostrum Length (RL), Rostrum Breadth (BRO), Least Interorbital Breadth (LIB), Orbital Length (ORL), Zygomatic Breadth (ZB), Breadth of Braincase (BB), and Breadth of the Zygomatic plate (BZP) (Fig. 1). The definitions of these measurements were the same as in Voss (1988) and Hershkovitz (1991). M1M is the distance between the labial side of first upper molars; BRO is the greatest breadth of the rostrum, and ORL is the greatest internal diagonal distance of the orbit (Fig. 1). Cranial and dental measurements were taken with digital callipers and are summarized in table 1.

For morphometric analysis, we exclusively considered adult animals (with all teeth erupted and functional). The following statistics were used: Analysis of Variance with LSD test for contrasting means, Canonical Discriminant Analysis, and Principal Components Analysis using pooled within-group covariance matrix of logarithmic variables.

Table 1. Sample size, mean, standard deviation, and range of cranial variables. See methods to variables abbreviation. n = total sample size.

	O. stramineus sp. n. n=36	*O. chacoensis* n= 5	*O. delticola* n=8	*O. nigripes* n=35	*O. fornesi* n=26	*O. flavescens* n=41	*O. microtis* n=46
GSL	33 25.7±1.1	3 23.8±0.6	7 25.0±1.3	31 25.5±1.3	25 22.8±0.8	38 22.5±1.1	35 23.5±1.1
	(23.3-28.3)	(23.2-24.3)	(23.2-26.3)	(23.1-28.4)	(21.0-24.0)	(20.1-24.3)	(21.1-26.0)
CIL	34 23.2±1.1	3 21.2±0.7	7 22.6±1.3	31 22.9±1.3	25 20.3±0.8	41 20.0±1.0	40 20.8±1.4
	(20.4-25.8)	(20.6-21.9)	(20.7-24.0)	(20.7-25.9)	(18.7-21.6)	(17.4-22.0)	(17.6-23.8)
BOC	33 5.7±0.2	3 5.7±0.3	7 5.9±0.3	33 5.7±0.2	25 5.4±0.2	41 5.4±0.2	36 5.6±0.2
	(5.4-6.1)	(5.5-6.0)	(5.5±6.3)	(5.3-6.5)	(5.1-5.9)	(5.2-5.8)	(5.0-6.2)
LD	36 6.4±0.4	5 5.7±0.5	8 6.2±0.4	35 6.3±0.4	26 5.6±0.3	39 5.4±0.4	45 5.7±0.5
	(5.3-7.5)	(5.2-6.3)	(5.6-6.7)	(5.4-7.6)	(5.0-6.2)	(4.5-6.0)	(4.4-6.5)
PB	36 4.7±0.3	5 4.1±0.2	8 4.4±0.4	34 4.5±0.3	26 4.0±0.2	41 3.8±0.2	44 4.2±0.3
	(4.2-5.4)	(3.8-4.2)	(3.8-4.8)	(3.9-5.2)	(3.6-4.5)	(3.1-4.2)	(3.3-4.9)
LM	36 3.7±0.2	5 3.5±0.1	8 3.4±0.2	35 3.7±0.1	26 3.1±0.2	41 3.2±0.1	45 3.1±0.1
	(3.3-4.2)	(3.3-3.7)	(3.2-4.0)	(3.5-4.0)	(2.8-3.6)	(3.0-3.5)	(2.7-3.5)
LIF	36 4.9±0.4	5 4.1±0.3	8 4.6±0.3	35 4.8±0.3	26 3.9±0.3	41 4.3±0.3	46 3.7±0.3
	(4.2-5.7)	(3.9-4.5)	(4.1-5.3)	(4.1-5.9)	(3.4-4.9)	(3.4-4.9)	(3.2-4.6)
BIF	36 1.8±0.2	5 1.6±0.1	8 1.7±0.1	35 1.8±0.1	26 1.7±0.1	41 1.5±0.1	46 1.6±0.2
	(1.5-2.4)	(1.4-1.8)	(1.6-1.9)	(1.5-2.1)	(1.4-1.9)	(1.3-1.8)	(1.3-2.0)
M1M	35 4.7±0.2	5 4.5±0.1	8 4.6±0.2	35 4.6±0.2	25 4.2±0.2	41 4.2±0.2	46 4.3±0.2
	(4.3-5.3)	(4.5-4.6)	(4.3-5.0)	(4.3-5.1)	(3.9-4.6)	(3.8-4.5)	(3.8-4.9)
BM1	36 1.1±0.1	5 1.1±0.1	8 1.1±0.1	35 1.1±0.1	26 0.9±0.1	41 1.0±0.1	45 1.0±0.1
	(1.0-1.3)	(1.1-1.2)	(1.0-1.2)	(1.0-1.2)	(0.8-1.1)	(0.9-1.1)	(0.8-1.2)
BL	35 3.5±0.3	3 3.5±0.1	8 3.4±0.2	31 3.5±0.2	25 3.1±0.3	41 3.1±0.2	42 3.0±0.2
	(2.8-4.1)	(3.3-3.6)	(3.1-3.8)	(3.1-3.9)	(2.5-3.8)	(2.9-3.6)	(2.5-3.4)
CH	36 7.8±0.3	5 7.5±0.2	8 7.6±0.4	35 7.8±0.3	25 7.0±0.3	41 7.1±0.3	46 7.1±0.3
	(7.3-8.4)	(7.2-7.8)	(7.1-8.1)	(7.3-8.8)	(6.5-7.5)	(6.5-8.0)	(6.3-8.4)
RL	35 9.3±0.6	4 8.7±0.6	8 8.9±0.5	35 9.1±0.7	26 7.9±0.4	38 7.6±0.5	42 8.1±0.6
	(7.8-10.7)	(8.3-9.5)	(7.9-9.6)	(7.7-10.6)	(7.3-8.7)	(6.4-8.6)	(6.3-9.1)
BRO	35 4.7±0.3	5 4.5±0.3	8 4.4±0.2	35 4.6±0.3	26 4.1±0.2	40 4.1±0.3	46 4.3±0.3
	(4.2-5.6)	(4.2-4.8)	(4.1-4.7)	(4.0-5.4)	(3.7-4.7)	(3.5-4.5)	(3.4-5.0)
LIB	36 3.8±0.1	5 3.9±0.1	8 3.6±0.2	35 3.8±0.2	25 3.7±0.2	41 3.4±0.2	46 3.8±0.2
	(3.5-4.0)	(3.8-4.0)	(3.4-3.8)	(3.5-4.1)	(3.3-4.2)	(3.2-3.9)	(3.4-4.1)
ORL	36 8.8±0.4	5 8.3±0.2	8 8.4±0.5	35 8.7±0.3	26 7.7±0.4	41 7.6±0.4	46 8.0±0.5
	(7.6-9.6)	(8.0-8.5)	(7.7-8.8)	(8.1-9.5)	(6.8-8.6)	(6.6-8.2)	(6.5±8.9)
ZB	36 13.2±0.6	4 12.8±0.3	8 13.0±0.6	35 13.3±0.6	26 12.0±0.6	37 12.0±0.7	44 12.1±0.7
	(11.9-14.8)	(12.3-13.1)	(12.2-14.0)	(12.3-14.9)	(10.5-12.8)	(10.3-13.3)	(10.2-13.5)
BB	35 10.7±0.4	3 10.6±0.1	7 10.6±0.3	32 10.9±0.3	24 10.0±0.4	41 10.1±0.3	45 10.2±0.4
	(10.1-11.6)	(10.4-10.6)	(10.1-11.1)	(10.2-11.5)	(9.1-10.7)	(9.5-11.0)	(9.4-11.6)
BZP	36 2.8±0.2	5 2.4±0.3	8 2.6±0.2	34 2.6±0.2	26 2.3±0.1	40 2.2±0.2	46 2.2±0.1
	(2.3-3.5)	(1.9-2.7)	(2.4-2.9)	(2.1-3.0)	(2.0-2.5)	(1.8-2.6)	(1.8-2.4)

Results

Karyotypic analysis of 16 *Oligoryzomys nigripes* showed 2n = 62/ FN = 81–82. This variation in fundamental number was due to a polymorphism resulting from an inversion in one member of pair no. 3. Five *O. flavescens* showed 2n = 64/FN = 68 while 8 *O. fornesi* showed 2n = 62/FN = 64.

Karyotypic analysis of 30 *O. stramineus* sp.n. showed 2n = 52/FN = 68 (Fig. 2). The autosomal complement is composed of 9 pairs of biarmed chromosomes (2 large pairs of metacentrics, 5 medium-sized pairs of metacentrics, and 2 small pairs of metacentrics) and 16 pairs of acrocentrics (1 large pair and other 15 pairs varying gradually in size from medium to small). The X chromosome is a large-sized submetacentric, and the Y chromo-

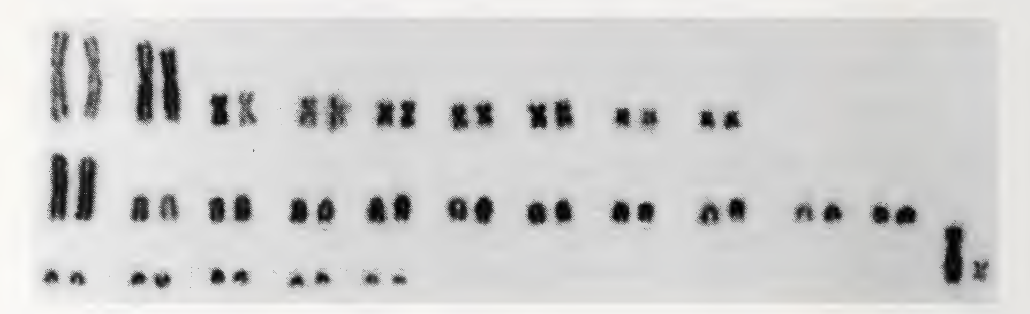


Fig. 2. *Oligoryzomys stramineus* sp. n. karyotype.

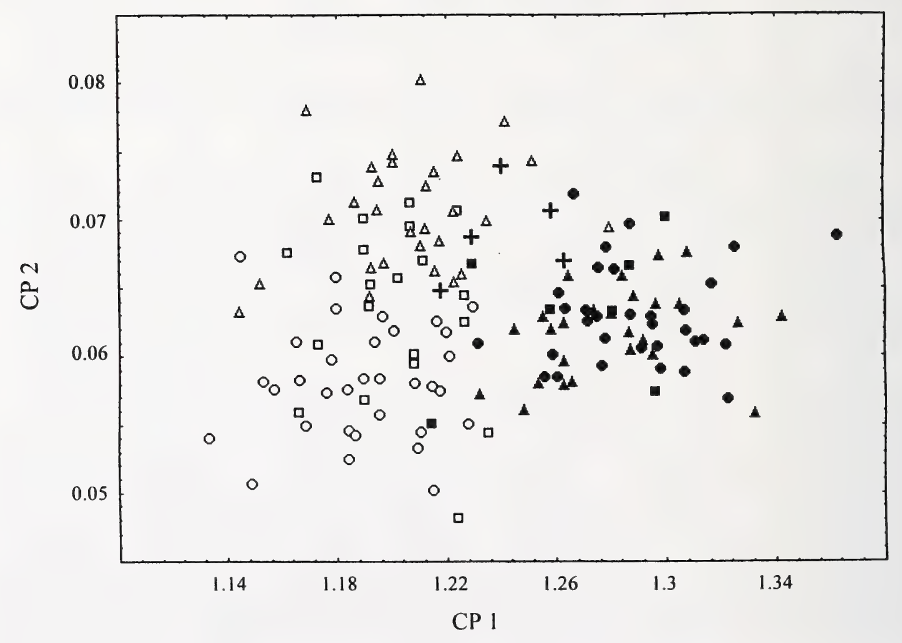


Fig. 3. Scores of the first two principal components (CP) extracted from the pooled within-group covariance matrix of log transformed measurement data: ● *Oligoryzomys stramineus* sp. n., ■ *O. delticola*, ▲ *O. nigripes*, ✚ *O. chacoensis*, △ *O. microtis*, □ *O. fornesi*, and ○ *O. flavescens*. The eigenvalues of the first two principal components are 0.102 (CP1) and 0.010 (CP2), corresponding to 70.6% and 7.1% of total variance.

some a medium-sized metacentric. Three specimens of *O. stramineus* sp. n. from Terezina de Goiás showed 2n = 52/FN = 69 due to a pericentric inversion in one chromosome of a small acrocentric pair.

In morphometric analysis, we grouped together males and females of all species because in *O. stramineus* sp. n., no significant sexual dimorphism was detected (t test). Principal Components Analysis (Fig. 3) grouped *O. nigripes*, *O. delticola* (Thomas, 1917), *O. chacoensis*, and *O. stramineus* sp. n. apart from *O. fornesi*, *O. microtis*, and *O. flavescens*. This separation occurred in the plane of the first principal component. Among species of the first group, *O. chacoensis* was closest to those of the second group. As the Principal Components Analysis separated two well delimited groups, one composed by small-sized species with yellow belly and another, of large-sized species with a white belly including *O. stramineus* sp. n., further analyses were carried out in this latter group.

Within the large-sized group, Canonical Discriminant Analysis discriminated three groups, (1) *O. nigripes* and *O. delticola*, (2) *O. chacoensis*, and (3) *O. stramineus* sp. n. (Fig. 4). Analysis of Variance between *O. nigripes*, *O. delticola*, *O. chacoensis*, and *O. stramineus* sp. n. showed significant differences in 10 cranial characters (GSL: $F = 2.99$, $p = 0.04$; CIL: $F = 3.62$, $p = 0.02$; LD: $F = 3.45$, $p = 0.02$; BP: $F = 3.99$, $p = 0.01$; LM: $F = 5.09$, $p = 0.004$; LIF: $F = 7.83$, $p = .0002$; BIF: $F = 2.94$, $p = 0.04$; LIB: $F = 4.58$, $p = 0.007$; ORL: $F = 2.82$, $p = 0.05$; BZP: $F = 3.27$, $p = 0.03$). LSD test ($p < 0.05$) showed that *O. stramineus* sp. n. was significantly different from: *O. chacoensis* in 9 variables (GSL, CIL, LD, BP, LM, LIF, BIF, ORL, BZP), *O. delticola* in 2 variables (LIB, ORL), and *O. nigripes* in 2 variables (LIB, BZP). This analysis also showed that *O. delticola* differed from *O. nigripes* in 2 variables (LIB, ORL) and from *O. chacoensis* in 2 variables (LM, LIB). Finally, *O. chacoensis* differed from *O. nigripes* in 8 variables (GSL, CIL, LD, BP, LM, LIF, BIF, ORL).

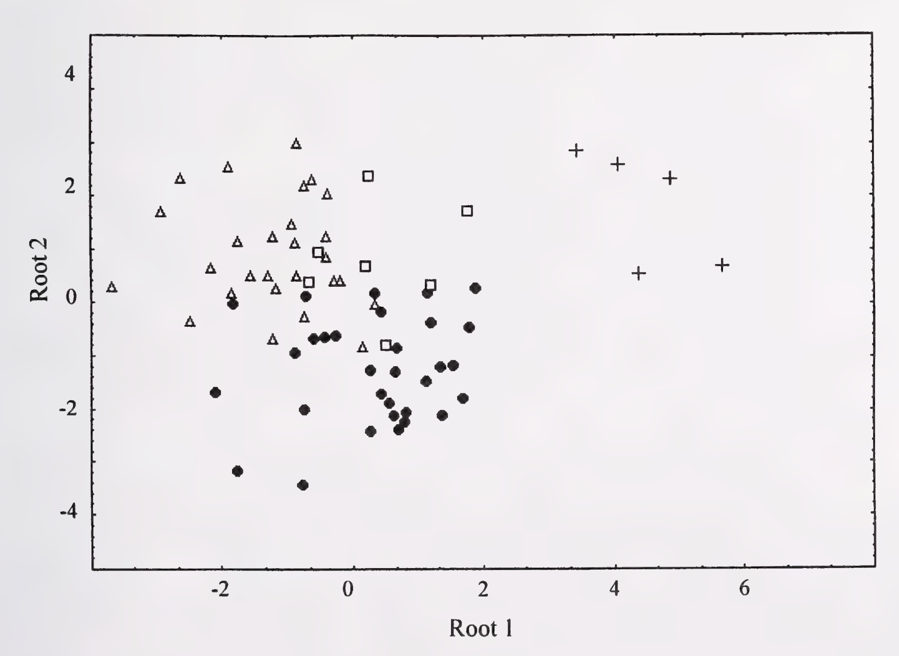


Fig. 4. Plot of the first two Canonical Discriminant Functions: Symbols are ● *Oligoryzomys stramineus* sp. n., □ *O. delticola*, △ *O. nigripes*, ✚ *O. chacoensis*. The eigenvalues of the canonical functions are 2.12 (CF1) and 1.41 (CF2).

Discussion

Karyological considerations

The 2 n = 62/FN = 81–82 karyotype herewith reported in *O. nigripes* is similar to the one found in specimens captured near its type locality in Paraguay by Myers and Carleton (1981) who considered this karyotype as characteristic of this species. A similar karyotype, however, was also found in animals captured in the type locality of *O. delticola* (Espinoza and Reig 1991), indicating that *O. delticola* and *O. nigripes* are karyotypically similar. Furthermore, specimens from São Paulo State (Yonenaga et al. 1976), captured near the type locality of *O. eliurus*, were also karyotypically similar to *O. delticola* and *O. nigripes*. In this latter species, chromosome polymorphisms were reported (2 n = 62/FN = 79 to 82) due to pericentric inversions in pairs nos. 3, 4 and/or 8 (Yonenaga et al. 1976; Almeida and Yonenaga-Yassuda 1991). These findings are coincident with ours in showing pericentric inversions in pair no. 3 of *O. nigripes*. Comparative karyological data indicate that all the above mentioned species comprise a karyomonomorphic group clearly apart from *O. stramineus* sp. n. (2 n = 52/FN = 68).

The 33 specimens of *O. stramineus* sp. n. here karyotyped showed 2 n = 52/FN = 68–69 similar to specimens from Paraíba and Pernambuco states karyotyped by Furtado (1981). Moreover, a single specimen (USMN 528416) from Exú, Pernambuco State, considered to be *O. chacoensis* by Carleton and Musser (1989), showed 2 n = 52/FN = 70 (Gardner, pers. comm.); this difference in fundamental number being apparently due to an inversion in a small acrocentric pair. On the other hand, all 16 specimens of *O. chacoensis* studied by Myers and Carleton (1981) showed 2 n = 58/FN = 74. Karyological comparisons between *O. stramineus* sp. n. and *O. chacoensis* showed differences in diploid and fundamental number and in the size of biarmed and acrocentric chromosomes. *O. stramineus* sp. n. has 2 pairs of large metacentric chromosomes approximately twice as large as any other of the 7 pairs of biarmed chromosomes while *O. chacoensis* has only 1 large pair of metacentric chromosomes approximately twice as large as any other of the 8 pairs of biarmed chromosomes. Additionally, the number of acrocentric chromosomes differs between species; corresponding to 16 pairs in *O. stramineus* sp. n. and to 19 pairs in *O. chacoensis*. These differences confirmed that *O. chacoensis* and *O. stramineus* sp. n. are karyologically different, as to be expected in different species.

In *O. longicaudatus*, Gallardo and Patterson (1985) found 2 n = 56/FN = 66 and 2 n = 54/FN = 66. These karyotypic differences were explained by a fusion event involving two acrocentric chromosomes of 2 n = 56 producing a large biarmed chromosome in 2 n = 54. Karyological comparisons between *O. stramineus* sp. n. and 2 n = 54 *O. longicaudatus* showed clear differences in diploid and fundamental number as well as in chromosome morphology. *O. stramineus* sp. n. has 2 additional biarmed chromosome pairs (one large-sized and another small-sized), and a large-sized acrocentric pair without recognizable counterparts in *O. longicaudatus*.

The *O. flavescens* karyotype (2 n = 64–66/FN = 66–68) was described by Sbalqueiro et al. (1991); variations in diploid number being due to presence of up to 2 B-chromosomes that, in specimens with 2 n = 65, behaved as univalents in first meiotic divisions. Similar variations were found in *O. flavescens* captured at its type locality (Brum-Zorrila et al. 1988) as well as in São Paulo State (Yonenaga et al. 1976; Kasahara 1978). Karyological comparisons (Sbalqueiro et al. 1991) indicated that this karyotype was indistinguishable from the one found in specimens captured in Paraguay (2 n = 64–66) which had been identified as *O. fornesi* by Myers and Carleton (1991). The *O. flavescens* here studied showed 2 n = 64/FN = 68 instead of 2 n = 64/FN = 66 as previously reported (Sbalqueiro et al. 1991). This difference in fundamental number can be explained by an inversion resulting in one small metacentric pair.

O. fornesi showed 2n = 62/FN = 64. Comparative karyological data indicate that *O. fornesi* and *O. flavescens* are clearly different from *O. stramineus* sp. n. (2n = 52/FN = 68).

Morphological considerations

Morphological and morphometric analyses showed that *O. stramineus* sp. n. differed from other species herewithin studied. *O. stramineus* sp. n. belongs to the large-sized group, being more similar in size to *O. nigripes* and *O. delticola*. *O. stramineus* sp. n. differs from *O. nigripes*, *O. delticola*, and *O. eliurus* by the following characters: (1) larger zygomatic plate resulting in a deeper zygomatic notch, (2) broader external wall of groove of infraorbital branch of the stapedial artery in the parapterygoid plate, (3) incisive foramen reaching or extending across plane delimited by first molars at all ages, contrary to the other 3 species in which this only occurs in young animals, (4) paler overall pelage color. It differs from *O. chacoensis* by the following characters: (1) larger body size, (2) more pronounced angular fossa, and (3) karyotype. It also differs from *O. longicaudatus* by its karyotype. Comparisons with other *Oligoryzomys* species were less important because their distributional limits are distant from the geographic distribution of *O. stramineus* sp. n.

O. stramineus sp. n. differs from *O. fornesi*, *O. microtis*, and *O. flavescens* by the following characters: (1) larger size, (2) whitish ventral color, (3) sharper contrast between ventral and lateral body parts, (4) shorter incisive foramen (only in respect to *O. flavescens*), and (5) karyotype.

O. fornesi was considered a junior synonym of *O. microtis* by Olds and Anderson (1987) and Carleton and Musser (1989). However, we consider *O. microtis* and *O. fornesi* as valid species on the basis of: (1) Principal Components Analysis, separating *O. microtis* from *O. fornesi* in the plane of CP2; (2) use of different habitat, because *O. fornesi* is predominantly distributed in open vegetational formations and *O. microtis* mainly occupies areas of forest formations; (3) molecular data, showing *O. fornesi* and *O. microtis* within separate clades (Myers et al. 1995).

We found morphological differences between specimens with 2n = 62 (*O. fornesi*) and 2n = 64–66 (*O. flavescens*), like a smaller incisive foramen (not reaching plane of first molar) in the former, and a larger one (reaching the plane of first molar) in the latter. These findings were confirmed in several specimens examined by us and previously karyotyped by Myers and Carleton (1981); (USNM 124218, 133818, 133819 with 2n = 62/FN = 64, and USNM 124216, 124217, 124222, 124255, 133816, 133833, 134341, 134342 with 2n = 64–66/FN = 66–68). Myers and Carleton (1981), however, identified these specimens as *O. fornesi*. This identification is questionable in view of more recent reports and our karyological data showing that specimens with 2n = 64–66/FN = 66–68 belong to *O. flavescens* and those with 2n = 62/FN = 64 to *O. fornesi*. This karyologic difference is further supported by our morphological analysis.

Geographic considerations

In view of our findings, the distribution of *O. nigripes* is considerably larger than previously estimated by Musser and Carleton (1993). It extends through Northern Argentina, Paraguay and part of Brazil (in the Atlantic forest from Rio Grande do Sul State to Bahia State, in central Brazil in the Distrito Federal and Goiás State, and in Northeastern Brazil in Pernambuco and Paraíba states).

O. chacoensis was first considered to be distributed in Bolívia (Depto. Beni, Santa Cruz and Tarija), Argentina (Formosa) and southwestern Brazil (Mato Grosso State; Myers and Carleton 1981) and its distribution was later extended to Jujuy, Chaco and

Salta in Argentina, and Ceará and Pernambuco states in Brazil (Carleton and Musser 1989). It is, however, unlikely that this distribution extends to Pernambuco State because the single specimen (USNM 528416) studied by Carleton and Musser (1989) actually belongs to *O. stramineus* sp. n. (see comments in the description of the species).

Myers and Carleton (1981) extended the geographic distribution of *O. fornesi* to São Paulo State on the basis of karyotypic data reported by Yonenaga et al. (1976). However, this is dubious in view that this karyotype (2 n = 64–66, FN = 66–68) is characteristic of *O. flavescens*. Later reports (Olds and Anderson 1987; Carleton and Musser 1989) considered *O. microtis* and *O. fornesi* as synonymous, thus extending the geographic distribution of *O. microtis* to Goiás State and Distrito Federal, Brazil. However, molecular and morphological evidence indicate *O. microtis* and *O. fornesi* as valid species, thus invalidating the extended distribution of *O. microtis* (specimens from Goiás State, Terezina de Goiás and Corumbá de Goiás, and Distrito Federal, Brasília showed morphological and karyological characteristics of *O. fornesi*).

O. stramineus sp. n. occurs in the Cerrado (Goiás and Minas Gerais states) and Caatinga (Paraíba and Pernambuco states), being sympatric with *O. nigripes* in Pirauá (Paraíba State), Bom Conselho (Pernambuco State), and Montes Claros (Minas Gerais State), and with *O. fornesi* in Terezina de Goiás (Goiás State), Bom Conselho, Correntes, and Macaparana (Pernambuco State) and Montes Claros (Minas Gerais State).

Oligoryzomys species are frequently sympatric, with the ocurrence of large-sized and small-sized species in the same locality (Thomas 1926; Langguth 1963; Myers and Carleton 1981; Svartman 1989). In the Cerrado of Central Brazil (Terezina de Goiás), we collected *O. fornesi* and *O. stramineus* sp. n. in the same habitat and trapline. In the Parque Nacional de Caparaó, we also collected *O. flavescens* and *O. nigripes* in the same habitat and trapline. In a transitional region between Caatinga and Cerrado in Minas Gerais State (Montes Claros), we collected *O. fornesi*, *O. nigripes*, and *O. stramineus* sp. n., though the latter two were not captured in the same habitat and trapline. Apparently, the forest formations of the Brazilian Atlantic forest contain, at least, two allopatric large-sized species with white belly, *O. nigripes* and *O. delticola*, and one small-sized species with yellow belly, *O. flavescens*, that is sympatric with either of the former. *O. nigripes* and *O. flavescens*, on the other hand, occur in the Cerrado of Central Brazil, but they have been collected in gallery forest, a link to the Atlantic forest. *O. nigripes*, moreover, also occurs in less dry areas of the Brazilian Caatinga. Two other species only occur in open vegetation formations (Cerrado and Caatinga): the large-sized white-bellied *O. stramineus* sp. n., and the small-sized yellow-bellied *O. fornesi*. *O. microtis* is distributed in the Amazonian forest. *O. chacoensis* occupies open vegetation formations from western Paraguay, SE Bolívia, Argentina, extending to Mato Grosso State, in Brazil (Myers and Carleton 1981).

On the basis of morphologic studies, karyologic data, and geographic distribution, *O. stramineus* sp. n. is herein described as a new species.

Oligoryzomys stramineus new species

Holotype: MN 34439, skin and skull of adult male collected by S. M. Lindbergh in 1991, field number CRB 607 (Figs. 5 and 6).

Other specimens examined: MN 46406, 46407, 46408, 46409, 46410, 46412, 46413, 46414, 46415, 46416, 46417, 46418, 46419, 46420, 46421, 46422, 46423, 46424, 46426, 46427, 46430, 46431, 46432, 46433, 46434 Terezina de Goiás, Goiás State, Brazil), LV-FC 10, 21 (Montes Claros, Minas Gerais State), UFPB-AL 2020 (Sítio José Camilo, Natuba, Paraíba State, Brazil), UFPB-LFS 49 (Pirauá, Paraíba State, Brazil), UFPB-AL 2049 (Vila Pirauá, Natuba, Paraíba State, Brazil), UFPB 1863 (Sítio Pau Vermelho, Correntes, Pernambuco State, Brazil), UFPB-PMN 360, 497 (Bom Conselho, Pernambuco State, Brazil), USNM 528416 (Exú, Pernambuco State, Brazil). All these specimens were karyotyped.



Fig. 5. Dorsal, ventral and lateral view of skull of *Oligoryzomys stramineus* sp. n. holotype (MN34439).

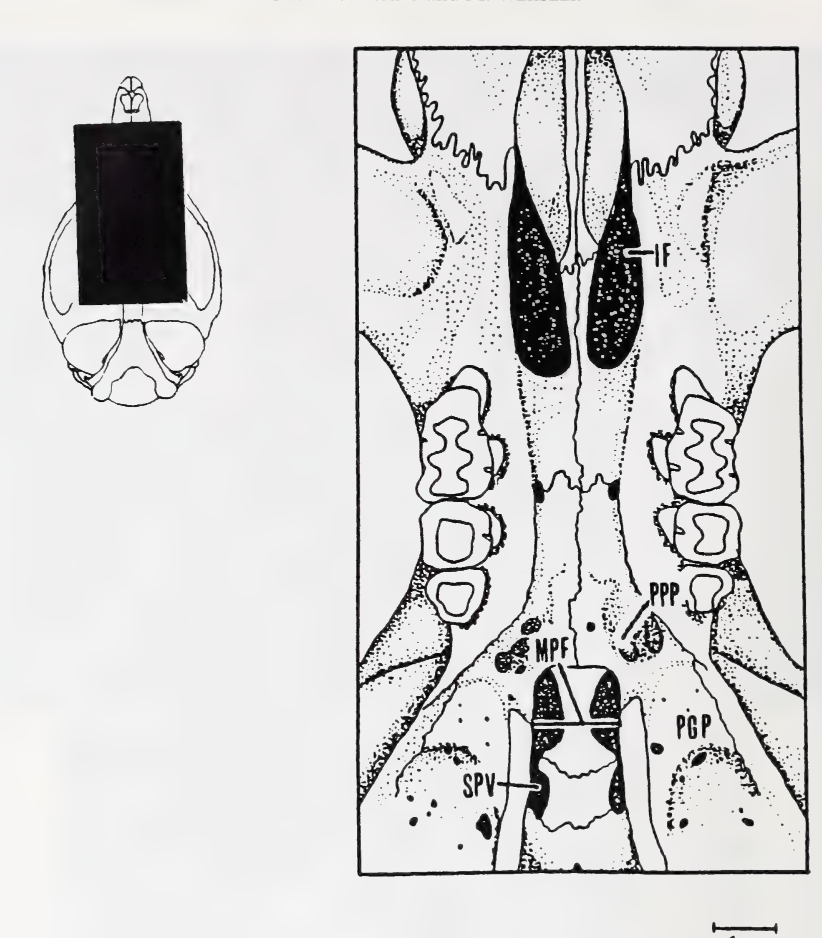


Fig. 6. Diastemal and palatal regions of the skull of *Oligoryzomys stramineus* sp. n. holotype (MN34439). IF, incisive foramen; MPF, mesopterygoid fossa; PPP, posterolateral pit; SPV, sphenopalatine vacuity; PGP, parapterygoid plate.

Type locality: Fazenda Vão dos Bois (13°34′29″S 47°10′57″W, 424 m), Terezina de Goiás, Goiás State, Brazil, 24 km N of Terezina, 15 km SW of Rio Paranã, a tributary of the upper Rio Tocantins, road GO-118, km 275.

Etymology: from *stramineus* (straw colored), referring to its orange pelage.

Distribution: from the Cerrado of Northen Goiás and Northen Minas Gerais states and the Caatinga of Paraíba and Pernambuco states, in Brazil (Fig. 7).

Diagnosis: a large-body-sized *Oligoryzomys* species with dorsal color paler than other species, whitish belly, long incisive foramen, broad zygomatic plate, unique diploid number ($2n = 52$).

Description:

External characteristics: Dorsum with three kinds of hairs: dark guard hairs, banded orange with plumbeous (basal half) overhairs, and soft gray underhairs. The mixture of dark guard hairs and orange overhairs accounts for a brownish-orange overall dorsum color in adult animals. In older animals, the pelage of the posterior part of dorsum is more orange-saturated than the anterior part, with a more homogeneous coloration. In young spe-

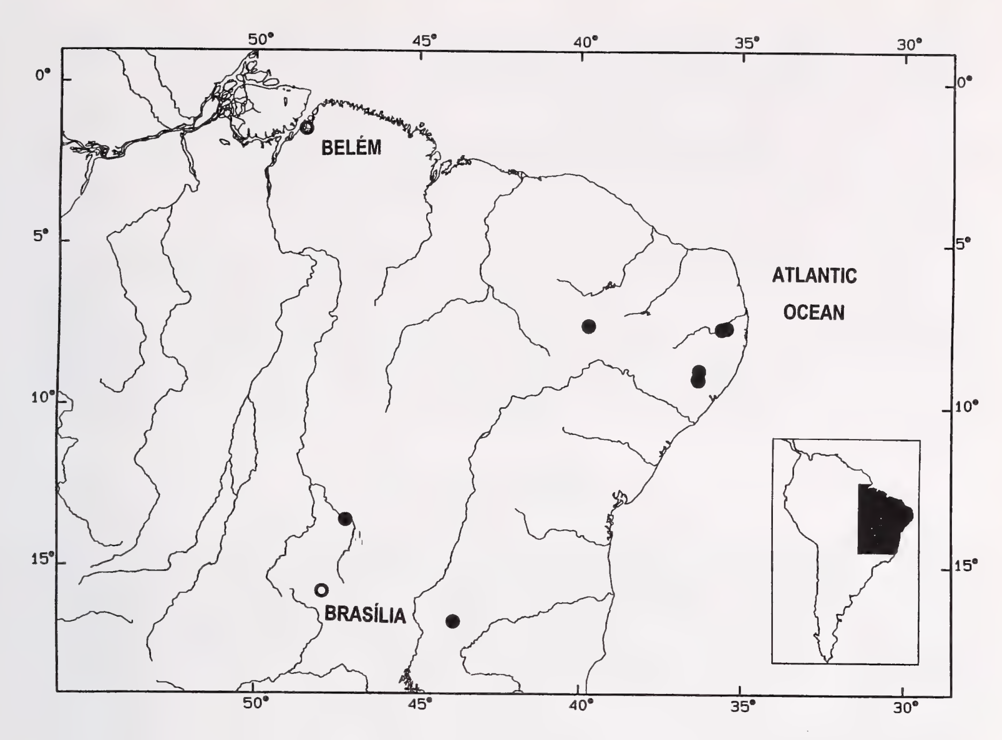


Fig. 7. Localities of occurrence of *Oligoryzomys stramineus* sp. n. (●).

cimens, the overall dorsal color is grayish-yellow and the overall pelage color has a more homogeneous appearance than in adults. Change from young to adult coloration starts laterally, reaches the central middorsum, and later expands to the anterior and posterior dorsum. Head with less orange than dorsum, and cheeks the same color as body sides. Dark ears with few brown orange hairs at inner side. Lateral body color clearly paler, with fewer dark guard hairs. Whitish ventral color with plumbeous basal part, except in chin and ventral side of neck where hairs are white at base. In young specimens, ventral color is beige and whitish. Contrast between ventral and lateral body parts variable among specimens, being more clearly delimited in adult specimens. Tail bicolor, upperparts with wholly gray dark hairs and underparts with lighter creamy hairs. In young specimens, the posterior ventral part or the whole ventral part of tail is gray. Tail with few thin hairs and apparent scales. Feet and limb underparts with white hairs, contrasting with brown orange color of superior parts.

Cranial characteristics: Interorbital region hourglass-shaped without supraorbital ridge. Postorbital ridge absent. Large interparietal, as broad as parietal. Rostrum and interorbital constriction similar in width. Large zygomatic plate without zygomatic spine, and with deep zygomatic notch. Jugal reduced or absent, zygomatic process of squamosal in contact with maxillary. Incisive foramen reaching or extending across plane of first molars (Fig. 6). Mesopterygoid fossa not reaching plane of third molars. Posterolateral pits varying in number, from single and small to multiple pits. Mesopterygoid fossa dorsally perforated by large sphenopalatine vacuities. Width of parapterygoid plate greater than width of mesopterygoid fossa (Fig. 6). Carotid circulation with pattern 2, as described by Voss and Carleton (1993), with large opening of stapedial foramen, lack of squamosal alisphenoid grove and sphenofrontal foramen. Medium or large subsquamosal fenestra

and large postglenoid foramen. Alisphenoid strut absent. Molar series parallel. Capsular projection of incisive alveoli prominent. Anteromedian flexus of M1 present but shallow.

External measurements: head and body length n = 33, mean = 94.3, sd = 10.2, range = 70–111; tail length n = 32, mean = 118.6, sd = 9.2, range = 95–134; hind feet n = 33, mean = 25.5, sd = 1.4, range = 23–29; ear length n = 32, mean = 16.1, sd = 1.6, range = 12–20. We did not detect sexual dimorphism in external measurements (t test). Cranial measurements are shown in table 1.

Karyotype: 2 n = 52/FN = 68–70.

Comparison with other species: see morphological considerations in discussion.

Comments: Carleton and Musser (1989) considered specimen USNM 528416 as *O. chacoensis.* We disagree for the following reasons: (1) karyotypic data, showing 2 n = 52/FN = 70 (Gardner, pers. comm.), different from the characteristic karyotype of *O. chacoensis* (2 n = 58/FN = 74; Myers and Carleton 1981); (2) cranial measurements, showing similar size as *O. stramineus* sp. n., and therefore larger than *O. chacoensis.*

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Zusammenfassung

Eine neue *Oligoryzomys*-Art aus Nordwest- und Mittel-Brasilien

Eine neue *Oligoryzomys*-Art aus Mittel-und Nordwest-Brasilien, *Oligoryzomys stramineus* sp. n., wird auf morphologischer Basis, biogeographischer und cytogenetischer Analyse beschrieben. Der Vergleich mit anderen *Oligoryzomys*-Arten zeigt zwei Artengruppen: die eine enthält größere Arten mit weißem Bauch (*O. chacoensis*, *O. nigripes*, *O. delticola* und *O. stramineus* sp. n.) und die andere Gruppe enthält kleinere Arten mit gelbem Bauch (*O. fornesi*, *O. microtis* und *O. flavescens*).

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Geographic variation of *Arvicanthis* (Rodentia, Muridae) in the Nile Valley

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Abstract

The size and shape differences in the skulls of nine populations of the rodents *Arvicanthis* along the Nile Valley (Egypt and Sudan) and one from Yemen were analysed. A three dimensional (x, y and z) landmark approach (Procrustes analysis) was used to study morphometric variation in these populations, in an attempt to evaluate differences between *A. niloticus* and *A. testicularis* and patterns of geographic variation. Size and shape differences were correlated to "ecogeographic" parameters (latitude, longitude, rainfall, temperature). Morphometric variation suggests that the two taxa have diversified in this area, and that variation reflects adaptation to current conditions. However, Partial Least Squares analysis showed that patterns of size and shape changes are different across species which suggests an independent evolutionary history.

Key words: *Arvicanthis*, geographic variation, geometric morphometrics

Introduction

Arvicanthis is a diurnal African rodent widespread in Egypt, Sudan, West, Central, East, and the Horn of Africa. It occurs in a great variety of habitats from sub-Saharan regions to Afroalpine moorlands, including croplands. However, the taxonomy of the genus is still provisional, as reflected by partial disagreements in the two most recent check lists of mammalian species (Corbet and Hill 1991; Musser and Carleton 1993).

Among the controversies, there is one which concerns the species occurring along the Nile Valley, from Egypt to Sudan and northern Ethiopia. According to Delany (1971), two species, *A. niloticus* and *A. testicularis*, occur in this area (the latter being considered synonymous to *A. dembeensis* by Corbet and Hill 1991, and synonymous to *A. niloticus* by Musser and Carleton 1993, who, however, include also *A. dembeensis* in this species). In a recent study, Philippi (1994) investigated cytogenetics and albumin and transferrin electrophoretic patterns in some animals from Cairo and Khartoum, and concluded that there are no differences and that individuals can reproduce. Furthermore, Philippi (1994) suggested that, although populations can be distinguished through a multivariate evaluation of skull linear measurements, this does not prove the occurrence of different species. However, patterns of geographic variation were not investigated and this may be important in assessing systematic relationships.

The aim of this study was to investigate the morphological variation in the form of the skull from populations of *Arvicanthis* along the Nile Valley, in an attempt to eventually distinguish between *A. niloticus* and *A. testicularis* and to explore patterns of geographic variation.

Rather than using traditional multivariate morphometrics, a landmark base approach, the core of geometric morphometrics (Bookstein 1991), was used. The new method of geometric morphometrics allows the recovery of the geometric properties of the skull in a Cartesian space, because morphological features are recorded as x, y and z co-ordinates. The 3-dimensional structure of the skull is thus preserved. This is advantageous because when using linear measurements typical of traditional morphometrics the 3-dimensional structure is lost. Moreover, three dimensional co-ordinates can be used for the statistical estimate of size and shape differences (after proper scaling, translation and rotation) as well as for their graphical visualisation (see, for a review, Rohlf and Marcus 1993; and Marcus and Corti 1996).

Material and methods

A total of 103 specimens from three populations in Egypt (Cairo, Asyut, and Aswan), six from Sudan (Merowe, Khartoum, Blue Nile, Kaka, Yuba, and Darfur) and one from Yemen (Lahej) were examined (Fig. 1; Tab. 1). Museum labels were used for species identification, and hereafter the names *A. testicularis* and *A. niloticus* will be used. The specimens of *A. niloticus* are from Egypt and Yemen and from the Blue Nile in Sudan; *A. testicularis* are all from Sudan. Individuals of *A. niloticus* and *A. testicularis* from the Khartoum area will be referred, respectively, as Khartoum(N) and Khartoum(T).

Specimens come from the collections of the British Museum of Natural History (London) and the Museo di Anatomia Comparata, Università di Roma 'La Sapienza'.

Four age classes were determined on the basis of molar tooth-wear, according to the amount of dentine exposure (Delany 1971).



Fig. 1. Geographic location of the populations studied. Filled squares: *A. niloticus*; open circles: *A. testicularis.* The inset shows the approximate range of the genus *Arvicanthis.*

Table 1. Species, populations, geographic location, number of males and females (M/F), and the "ecogeographic" parameters recorded. MAT: Mean Annual Temperature; MJT: Mean July Temperature; MJaT: Mean January Temperature. MAR: Mean Annual Rainfall; MJR: Mean July Rainfall; MJaR: Mean January Rainfall (rainfall in mm). Dry: number of dry days during the year; Semi-dry: number of semi-dry days during the year; Humid: number of humid days during the year.

Species	Population	Latitude	Longitude	M/F	MAT	MJT	MJaT	MAR	MJR	MJaR	Dry	Semi-dry	Humid
A. niloticus	Asyut	27°03′ N	31°01′ E	3/5	22.9	30.0	13.5	0	0	0	365	0	0
	Aswan	24°02′ N	32°53′ E	2/4	26.9	34.0	16.7	1	0	0	365	0	0
	Blue Nile	11°47′ N	34°23′ E	8/8	28.1	31.7	26.0	736	384	0	242	80	43
	Cairo	30°03′ N	31°13′ E	7/8	20.5	34.7	12.2	19	0	11	365	0	0
	Khartoum	15°36′ N	32°33′ E	3/4	29.7	34.3	23.8	158	123	0	365	0	0
	Lahej	13°10′ N	45°00′ E	4/3	27.6	31.2	24.1	62	23	2	365	0	0
A. testicularis	Darfur	13°27′ N	25°20′ E	7/5	25.7	30.5	20.0	283	215	0	315	36	14
	Kaka	11°45′ N	32°47′ E	7/3	27.5	31.2	24.3	528	272	0	259	69	37
	Khartoum	15°36′ N	32°33′ E	4/5	29.7	34.3	23.8	158	123	0	365	0	0
	Merowe	19°10′ N	29°20′ E	3/0	27.6	34.1	30.9	21	6	0	365	0	0
	Yuba	04°52′ N	31°36′ E	7/3	27.4	25.4	28.1	971	271	12	150	123	92

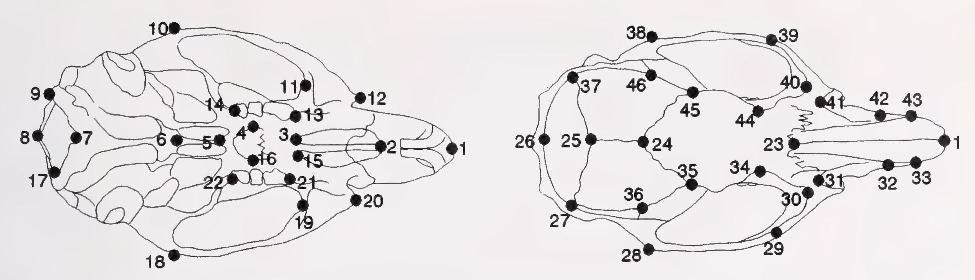


Fig. 2. The 46 landmarks collected as x, y, and z coordinates on the skull (shown from the dorsal and ventral view).

Images of the skull were obtained with a Sony CCD-F555E video-camera with a 10× zoom lens. The images were digitized through the VISIONplus-AT board (Imaging Technology Inc.). X and y co-ordinates were collected using the MTV software (Uptegraff 1990–1993). To reconstruct three dimensional x, y, z co-ordinates from two dimensional images, the images were collected at 0°, 45°, 120°, 180°, 240°, and 315° degrees, and three dimensional co-ordinates were then obtained from two dimensional co-ordinates by translation and rotation, resulting in 46 x, y, z landmarks (Fig. 2).

To avoid the effect of lateral asymmetry, the two sides of the skull were averaged and the y co-ordinates of landmarks located on the sagittal plane were set to zero. The averaged configurations were then reflected to obtain the complete representation of the skull.

The two components of the form, i. e. size and shape, were partitioned as follows. The centroid size, i. e. the square root ot the sum of the square of the distances of each landmark from the centroid (Bookstein 1991), was computed to best calculate the size of each specimen. Size differences between populations were tested by ANOVA (unbalanced design) and shown through box plot, excluding age class one.

Specimens were superimposed (translated, rotated, and scaled) over the consensus form through the Generalized Least Square Procrustes procedure (GLS; Rohlf and Slice 1990), using the GRF-nd program (Slice 1993). These new co-ordinates of the aligned specimens are standardised to unitarian centroid size; thus, they represent the shape component of the form and they were used for all statistical analyses of shape.

Sexual dimorphism in shape was estimated through MANOVAs (unbalanced design) for each landmark (x, y, z co-ordinates).

Eigenvalues and eigenvectors from the variance-covariance matrix of the new co-ordinates were extracted and used to investigate trends in variation. Shape changes associated to each eigenvector were visualised as displacements from the consensus using the program GRF-nd. This allows to relate the ordination of each principal component to a typical associated shape change.

A Model II ANOVA was performed following the Leamy (1983) procedure to test whether sex, age, and their interaction affect the principal components used to describe shape variation between species and populations. To visualise morphometric similarities between populations, a Minimum Spanning Tree was calculated from the Procrustes distances (Bookstein 1991).

As there is a clinal climatic variation along the Nile river with a dramatic aridity increase from Cairo to Merowe, the following geographic and climatological parameters were recorded (hereafter referred as "ecogeographic"): latitude and longitude; mean annual raintall (MAR), mean January rainfall (MJaR), mean July rainfall (MJR), all in mm; mean annual temperature (MAT), mean January temperature (MJaT), mean July temperature (MJT); number of dry, semi-dry, and rainy days during the year (Tab. 1). These data were collected from the F. A. O. Economist Intelligence Unit (1995).

Centroid size and shape for each individual were related to these parameters through multiple regression and Partial Least Square (PLS; Streissguth et al. 1993), respectively. PLS is a multivariate technique based on the singular value decomposition of the correlation matrix between two blocks or arrays of variables ("left" and "right" blocks), so that the predictive interrelations between the two are summarised by two sets of latent vectors, one for each block. In this case, the left block was represented by population scores on the first three principal components, and the right block by the geographic and climatic parameters.

The box plots were obtained using the STATISTICA program (1993), the Minimum Spanning Tree and the PLS with the NTSYS-PC program (Rohlf 1993) and all other statistical analysis using the SAS statistical package (1993).

Results

Analysis of size differences

Size differences between populations are significant ($F = 30.68$, $P < 0.001$). These differences are represented by the box plot in figure 3. In general, *A. niloticus* is larger than *A. testicularis*. Individuals of Asyut are significantly larger than other populations (with the exception of Blue Nile and Cairo), and the population of Lahej from Yemen is significantly different from the smallest populations, i. e. Merowe and Darfur.

The multiple regression of centroid size on geographic and climatic parameters suggested a general trend in size decrease from North to South. The vector representing the "ecogeographic" parameters is highly correlated with latitude ($r = 0.97$) and it is negatively correlated with the mean annual rainfall and mean annual temperature (respectively $r = -0.80$ and $r = -0.97$); the correlation with centroid size is 0.40 which indicates an overall significance of $P < 0.001$. Pearson's correlation coefficients and their significance calculated for centroid size and the "ecogeographic" parameters are shown in table 2. Separate analyses for the two species indicate, however, different directions of size change, as the "ecogeographic" vector is positively correlated with latitude in *A. niloticus* (0.99), whereas it has a negative correlation in *A. testicularis* (–0.97). As a result, size decreases southwards in *A. niloticus* and northwards in *A. testicularis*.

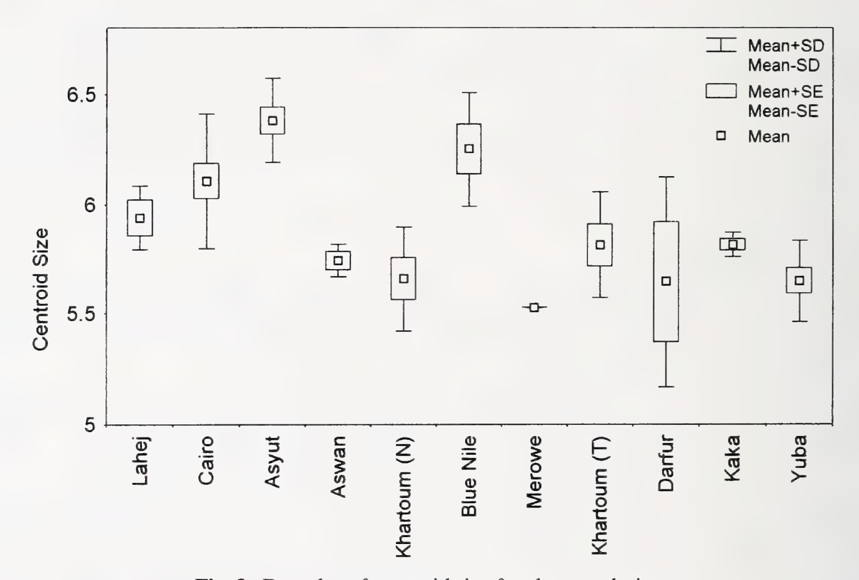


Fig. 3. Box plot of centroid size for the populations.

Analysis of shape differences

Sexual dimorphism in adults was tested through MANOVAs for each landmark, population by population (excluding Merowe, Sherik, and Lahej). Fourteen significant differences were found at $P < 0.05$ (Landmarks 2, 5, 7, 8, 12, 16, 19, 24, and 28 in Cairo; Landmarks 3, 24, and 29 in the Blue Nile; Landmarks 5 and 16 in Kaka; Landmark 15 in Asyut) out of the 203 landmarks tested. This effect was considered negligible and all further analyses were performed irrespective of sex.

Table 2. Relationships of size and shape with ecogeography. Column 2: multiple regression correlation coefficients of centroid size with the "ecogeographic" parameters (* = P < 0.05, ** = P < 0.001). Columns 3 and 4: Partial Least Squares, correlation of the original variables (the principal components from the Procrustes aligned specimens and the "ecogeographic" descriptors) with first shape end "ecogeographic" latent vectors.

	correlation coefficient	shape	ecogeography
Principal component 1		0.95**	0.50**
Principal component 2		0.23*	0.12
Latitude	0.44**	0.53**	0.94**
Longitude	0.05	0.40**	0.03
Mean annual rainfall	–0.12	–0.32*	–0.92**
Mean August rainfall	–0.16	–0.38*	–0.89**
Mean January rainfall	0.21*	0.24*	0.15
Mean annual temperature	–0.47**	–0.46**	–0.68**
Mean August temperature	–0.39**	–0.44**	–0.89**
Mean January temperature	0.08	0.28*	0.67**
Dry days / year	0.09	0.29*	0.87**
Semi-humid days / year	–0.14	–0.37**	–0.83**
Humid days / year	–0.03	–0.19	–0.83**

As shown in figure 4 A, the second principal component clearly represents an explanatory factor of the differences between age classes (the Pearson correlation coefficient is 0.646, P = 0.0001). This vector constitutes 12% of total variance, so it is a relatively important inter-individual variable. Shape differences associated to this second 'growth' vector are illustrated in figure 5 A: adults are characterised by a short rostrum, as well as by a braincase which is short and laterally restricted in correspondence to the sutures of parietals with the frontal bones. The lateral and frontal views of the skull highlight the process of shape change during growth. In fact the braincase profile becomes lower and it is laterally compressed, the orbits move slightly downward and the foramen magnum expands.

The first principal component represents 26% of the total variance and shows differences between populations and species (Fig. 4 A, B). This pattern is not affected by sex, age, and by their interaction, as shown by the model II ANOVA (F values are, respectively: 2.09, 0.90 and 0.79; all not significant).

The scatter plot of principal components one and two in figure 4 A shows the morphometric differences between species. Figure 4 B represents the ordination of population means onto principal component one and three, and suggests an opposite clinal trend in shape, as the scores of *A. testicularis* increase southwards while those of *A. niloticus* increase northwards. The third principal component (7% of total variance) describes differences between populations within *A. niloticus* and *A. testicularis.*

Morphometric relationships based on shape are shown by the Minimum Spanning Tree from the Procrustes distances (Fig. 4 B). Two main clusters are clearly evident, corresponding to the two species. It should be underlined that the Yemenite population of Lahej clusters with *A. niloticus.*

Differences between the two species are shown graphically as shape changes from the consensus in figure 5 B. *A. testicularis* is characterised by a backward shift and expansion of the post-parietal bones, a lowering of the vault, and an upward shift of the foramen magnum. Moreover, zygomatic arches of this species have moved upwards.

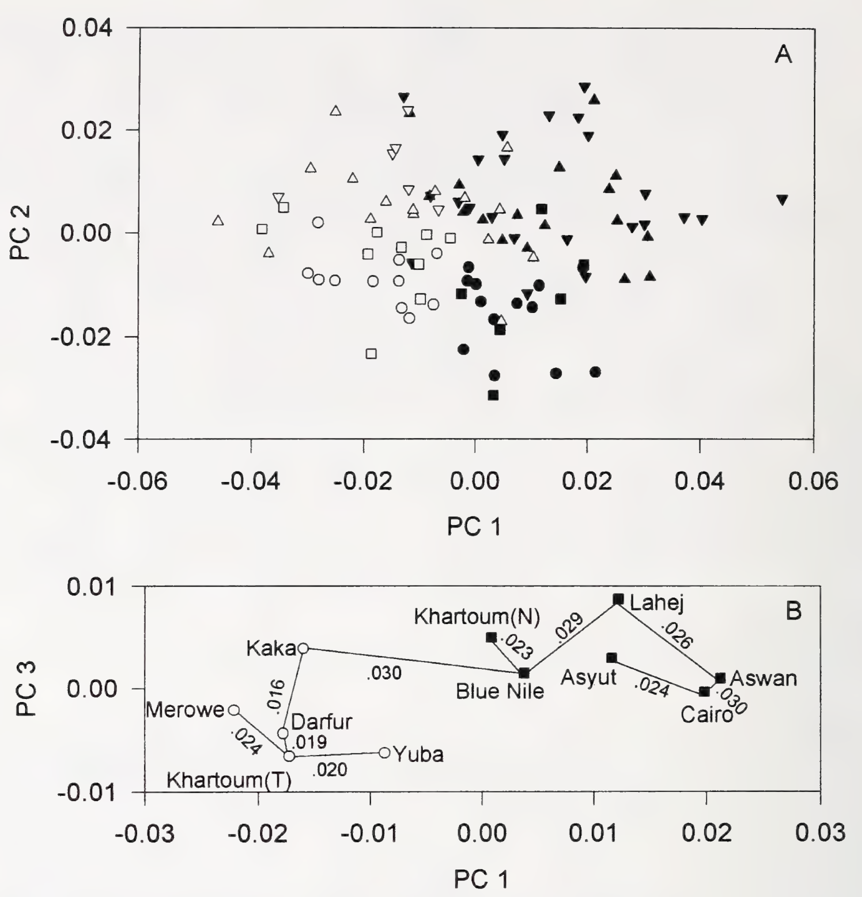


Fig. 4. Principal components analysis of the Procrustes aligned specimens. Part A: Scatter plot of the first two principal components; individuals are shown by age class and species. Circles, age class 1; squares, age class 2; triangles, age class 3; reversed triangles, age class 4; filled symbols are for *A. niloticus* and open symbols for *A. testicularis*. Part B: Scatter plot of first and third principal components, with population means only. A Minimum Spanning Tree is superimposed on the plot; numbers indicate segment lengths.

Partial Least Squares reveal a clear geographic pattern of variation in shape. Correlation between first, second, and third shapes and "ecogeographic" latent vectors are, respectively, 0.53, 0.26, and 0.15. The first shape latent variable is highly correlated to the first principal component computed on the Procrustes aligned specimens, and the first "ecogeographic" vector to latitude, mean annual rainfall, mean August temperature, and number of dry, semi-dry, and rainy days per year (Tab. 2). This first latent vector constitutes 73% of total variance.

Relationships between shape and ecogeography are shown in the scatter plot between first shape and "ecogeographic" vectors (Fig. 6). It suggests a pattern of morphometric variation in shape across populations from North to South. There is a gap at the level of Khartoum, where both species occur. They both have the same score for the first "ecogeographic" vector, but a very different score for the first shape vector. Moreover, separate PLS analyses for the two species show an inverse direction in shape change: scores on the shape latent vector increase from North to South in *A. testicularis* while they diminish in *A. niloticus*.

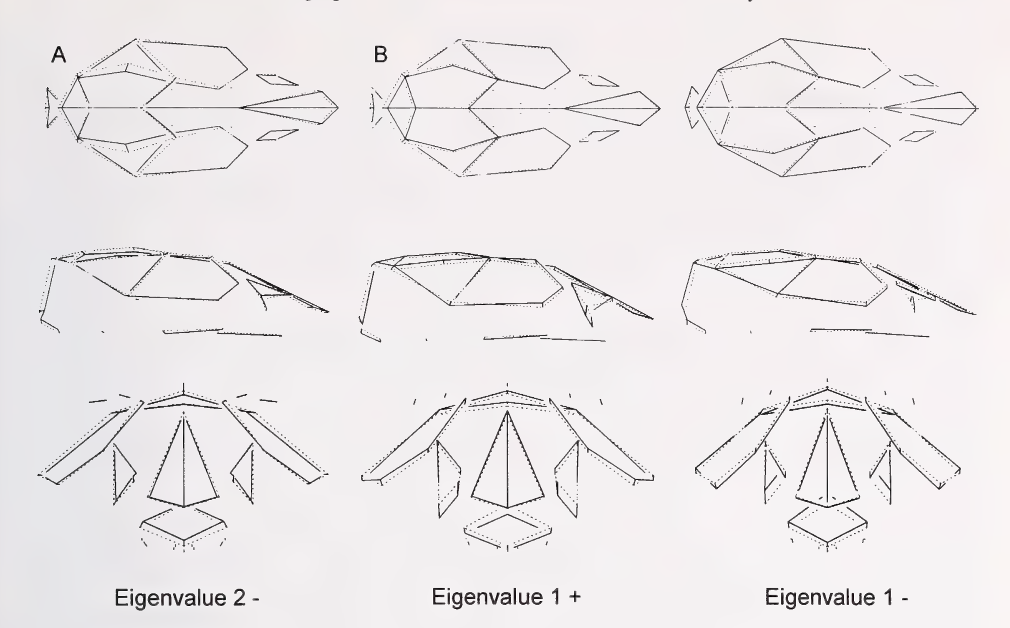


Fig. 5. Shape variation associated with the first two principal components. The dotted lines indicate the shape of the consensus (average), and the solid lines show the kind of shape change relatively to the consensus occurring in the positive (sign plus) and negative (sign minus) directions of eigenvector 1 and 2 (see Fig. 4, for the individual and population scores onto each eigenvector). Part A: Eigenvector 2 shows shape changes occurring from age class 1 (positive scores) to age class 4 (negative scores, the only shape shown). Part B: Eigenvector 1; shape changes from the consensus in *A. niloticus* (plus sign) and *A. testicularis* (minus sign). From top to bottom: upper, lateral, and frontal views of the skull.

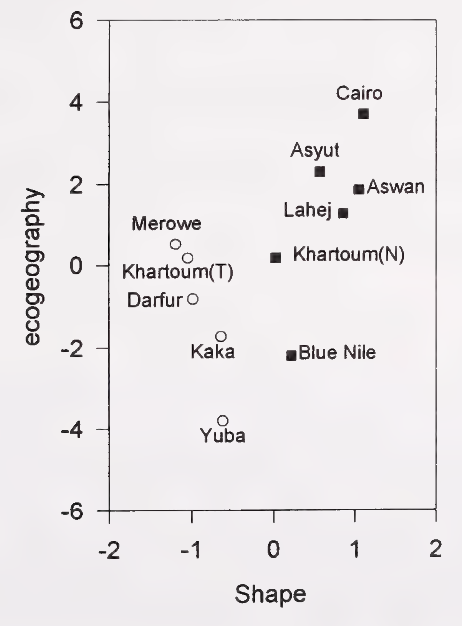


Fig. 6. Scatter plot of Partial Least Square between the first latent shape and "ecogeography" vectors; open circles: *A. testicularis*; filled squares; *A. niloticus* (population means are shown).

Discussion

There are two main points which merit a discussion: differences between age classes and populations, and the origin of morphometric variation across the Nile Valley and its systematics implications.

Pattern of shape changes during growth and of size and shape differences between populations were made possible by the decomposition of the form into its size and shape components. The relevance of shape variation due to different age can lead to misleading interpretations of the results. For this reason, shape variability according to age classes must be taken into account.

As far as the origin of morphometric variation is concerned, results indicate that variation in size and shape is clinal from North to South. This could be due to one lineage whose morphology progressively changes due to natural selection for current conditions, e.g. aridity, or to two separate, morphologically distinct phylogenetic lineages meeting parapatrically and forming a secondary contact area. The first explanation hypothesises an 'ecological cause'; the second a 'phylogenetic cause' (Endler 1986). If the ecological cause is correct, one would expect a continuous correlation from North to South between ecogeography and form. On the contrary, if the 'phylogenetic' explanation is correct, although a correlation between ecogeography and form would be expected in its entirety, there would however be an indication of different patterns within the two taxa.

The results favour the 'phylogenetic' rather than the 'ecological' explanation, both for size and shape variation. Size increases northwards in *A. niloticus* and southwards in *A. testicularis*, and the first shape latent vector is positively correlated with latitude in *A. niloticus*, while is negatively correlated in *A. testicularis*. Moreover, there are evident morphometric differences between populations of the two species occurring in the Khartoum area.

These different clinal patterns in size and shape change would reflect different pathways of range expansion in *A. niloticus* and *A. testicularis*, most probably after the Late Quaternary, when the Nile was a seasonal river (Adamson et al. 1980).

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Zusammenfassung

Geographische Variation von Arvicanthis (Rodentia, Muridae) im Niltal

Größen- und Formunterschiede von Schädeln der Nagergattung *Arvicanthis* wurden in neun Populationen aus dem Niltal (Ägypten und Sudan) und einer aus dem Jemen analysiert. Ein dreidimensionales (x, y, z) Landmarkensystem (Procrustes analysis) wurde benutzt, um die morphometrische Variation in diesen Populationen zu studieren und damit Differenzen zwischen *A. niloticus* und *A. testicularis* und zugrundeliegende Muster der geographischen Variation zu ermitteln. Größen- und Formunterschiede wurden mit geographischen Parametern (Länge, Breite, Niederschlag, Temperatur) korreliert. Die morphometrische Variation spricht dafür, daß in der untersuchten Region zwei Taxa vorkommen und daß deren Variation Anpassungen an die aktuellen Lebensbedingungen reflektiert. Die Analyse zeigt aber auch, daß die Größen- und Formunterschiede von Art zu Art differieren, was auf eine unabhängige Evolution deutet.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Plerotes anchietae (Seabra, 1900) in Malawi, Central Africa (Mammalia: Chiroptera)

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Key words: *Plerotes anchietae*, distribution, size, specific characters, teeth

In the Nyika National Park of northern Malawi, two small fruit bats were collected, which proved to be *Plerotes anchietae* (Seabra, 1900), as described and illustrated by ANDERSEN (1912) and reviewed by BERGMANS (1989). *P. anchietae* was not previously known from Malawi, where 59 species of bats are recorded (HAPPOLD et al. 1988; HAPPOLD and HAPPOLD 1997).

Note: THOMAS et al. (1994) examined *Nycteris nana* Andersen, 1912, from Malawi, which would represent an additional species, but the collecting site (KERSHAW 1992), catalogue number, and previous examination (CAKENBERGHE and VREE 1985) make it highly probable that this is actually *Nycteris woodi* ANDERSEN, 1914 (see HAPPOLD et al. 1988).

Information on *P. anchietae* is based on nine specimens only (BERGMANS 1989). The present material confirms and extends our knowledge about this rarely collected fruit bat.

The two specimens, an adult male and an immature female, were mistnetted simultaneously just before dawn (between about 04:00 and 5:00 h) on the 13th April 1997 in the Mondwe Valley (10°24′ S–33°50′ E) at an altitude of 1 760 m. Apparently, this pair was flying in company in the height of 2 m above ground above a high grass area from an open savanna-*Brachystegia*-woodland with little undergrowth towards a river. The collecting site confirms that *P. anchietae* has submontane to montane habitat preferences, with previous collecting sites situated between 1 000–1 500 m to 1 500–2 000 m altitude.

The known occurrence of this species is presently confined to high plateau areas in Angola in the west and in a disjunct eastern region in SE-Congo (Zaïre) and NE-Zambia. In Angola, *P. anchietae* is known from four localities (see BERGMANS 1989, who mapped only three sites).

In Shaba Province (formerly Katanga) of Congo/Zaïre, *P. anchietae* has been collected only from Upemba National Park. A second record from Congo/Zaïre by HAYMAN et al. (1966) from Panda (10°59′ S–26°47′ E, Shaba Prov.), based on a specimen in the collection of the Koninklijk Museum voor Midden Afrika, Tervuren (KMMA), was re-identified as an immature *Epomophorus* species (BERGMANS 1989). HAYMAN and HILL (1971) list *P. anchietae* from Likasi (formerly Jadotville, 10°59′ S–26°48′ E, Shaba Prov.). BERGMANS (1989) could find no specimen from this locality (quoting Likasi erroneously from HAYMAN et al. 1966) in its depository, also the KMMA. The co-ordinates given by HAYMAN et al. (1966) prove the collecting sites, Panda and Likasi, to be synonymous and concern the same specimen.

In Zambia, *P. anchietae* has been found in Abercorn (= Mbala, 08°51′ S–31°23′ E) and Kasama (10°13′ S–31°13′ E). The additional Malawi record is approximately 200 km east of the latter locality and presently documents the easternmost occurrence of the species. Doubtlessly, *P. anchietae* will be found in other highland areas of the Central African Rift Valley, as prognosed already by Kingdon (1974).

The two present specimens (SMF 85 744-5) are the first to be preserved in alcohol (skulls extracted, soft palate in situ, tongues and intestines saved). The male (being the first adult available of its sex), does not have epomophorine epaulettes, thus confirming Harrison's (1960) findings in a subadult male. In case this secondary sexual character might be seasonal, neither glandiferous skin nor an incipient invagination could be detected in its shoulder region. However, in both sexes there is a spot of white hairs at the base of the propatagium, its position not comparable to that of epaulettes in *Epomophorus* Bennett, 1836. These humeral spots had been described by Seabra (1900) but were not mentioned by Andersen (1912) and subsequently their significance as a species-specific character was not recognised any more. Both specimens posses the white moustache and beard first described by Bergmans (1989). There is no indication of cheek pouches, the inside of the upper lips being smooth (except for a papilla) and the cheek is not as elastically extendible as in *Epomophorus.*

The white marks at the posterior base of ears are not tufts, as they are customarily named and also described as such by Seabra (1900) for *P. anchietae.* They are white hairs lining the basal third to a half of the ear conch margin; this is also the case in the genus *Epomophorus* and *Epomops* Gray, 1870.

The nostrils are less tubular than they are in *Epomophorus.* Between the nostrils, a median furrow extends from the margin of the upper lip onto the snout attaining the level of the hind margin of the nostrils. In *Epomophorus* this furrow terminates shortly above the lower margin of the nostrils.

The tongue confirms to the description by Harrison (1960). Despite the tongue not being extensible, *P. anchietae* may possibly be a flower visitor. With its narrowed snout it can stick its head into larger flowers to reach nectar.

Several specific characters, like absence of tail, reduced uropatagium, humeral spots, absence of epaulettes, a moustache and a beard, morphology of the nose region, tooth formula, ridge pattern of soft palate, and shape of rostrum are divergent from the characters of epomophorine bats as originally defined by Andersen (1912) and including the genus *Plerotes* Andersen, 1910. A phylogenetic analysis of 33 anatomical characters of Megachiroptera by Springer et al. (1995) removes *Plerotes* from the *Epomophorus* section and transfers it to the *Rousettus* section.

External measurements, cranial dimensions (in mm) and weights (in g) are for the adult male (SMF 85 744) and immature female (SMF 85745) respectively:

Body: Head and body 70, 70; tails absent; hindfoot s. u. 11.3, 12.1; ear 17.8, 16.6; forearm 50.6, 46.5; tibia 20.2, 19.0; weight 20.0, 20.0. Wing: 1. digit metacarpal 7.5, 8.6; 1. digit 1. phalanx 8.8, 9.3; 2. digit metacarpal 25.1, 23.0; 2. digit 1. phalanx 9.7, 9.3; 3. digit metacarpal 35.1, 31.3; 3. digit 1. phalanx 26.6, 23.2; 3. digit 2. phalanx 35.0, 31.5; 4. digit metacarpal 35.2, 32.6; 4. digit 1. phalanx 20.2, 18.9; 4. digit 2. phalanx 19.6, 18.2; 5. digit metacarpal 34.0, 32.0; 5. digit 1. phalanx 17.5, 16.8; 5. digit 2. phalanx 17.2, 15.8. Skull: Greatest length of skull 28.23, 27.7; condylobasal length 26.84, 25.92; mastoid width 11.46, 12.18; width across zygomata 14.17, 14.36; interorbital width 5.26, 4.96; postorbital width 8.81, 8.01; width across upper canine at alveoli 5.96, 5.86; ibid. at crowns 6.24, 5.96; width across last upper molar 7.98, 8.03; upper toothrow length at crowns C^1–M^1 8.08, 7.53; ibid. at alveoli 7.94, 7.37; length of mandible 21.47, 20.74; mandible height 5.91, 5.51; lower toothrow length at crowns, male C_1–M_3 9.34, ibid. female C_1–M_2 8.39.

The male had testes measuring 4.6×2.5 mm. The female showed no reproductive signs, but developed nipples and slightly swollen surrounding area appeared to indicate

onset of sexual maturity. The uterus has not been opened for examination, but no embryo was apparent.

The above measurements, compared to those previously published (Bergmans 1989) do not indicate a sexual dimorphism. One generic character of *Plerotes*, the width across M^1–M^1 being larger than the toothrow length C^1–M^1 (see Andersen 1912; Bergmans 1989), is not conspicuous in the present specimens.

The male has the full set of teeth with M_3 present on both sides, both M_2 have two roots. In the female M_3 is absent from both sides, the right M_2 had been shed, its alveola is open; in the left M_2 the anterior and posterior roots are fused into a horizontally elongated single root.

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Presence of female *Myotis myotis* in nursery colonies

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Key words: *Myotis myotis*, nursery colonies, presence, colony size

Population densities and colony sizes of the greater mouse eared bat (*Myotis myotis*) have been reported for many parts of Central Europe (Hedergott 1993; Helversen et al. 1987; Horacek 1985; Hurka 1988; Roer 1986; Rudolph and Liegl 1990; Spitzenberger 1993; Tress et al. 1989 a, b, c). Most reports are based on counts of bats in nursery colonies which consist mainly of females and their offspring. However, not all specimens occupy the same diurnal roost every day (Roer 1988). In particular one year old females seem to be regularly absent from colonies. Only 16 to 54% of females born the previous year were present in summer colonies during counts at a number of sites (Haensel 1980; Horácek 1985; Oldenburg and Hackethal 1989; Roer 1968). However, in these cases the samples were taken once a year. Therefore the counts do not show how many females live in the colony, but how many are (on the average) present on a particular day. When bats do not return to the roost every day, a colony may be larger than indicated by a count on a specific visit.

In order to gain more information on the presence of female *Myotis myotis* at their rosts, I checked the presence of individually banded bats in colonies regularly each summer over a period of three years (1991–1993) in an area of 4 000 km^2 located in the southeastern part of Bavaria (47°49′N and 11°12′E) where 22 nursery colonies were known Zahn 1995). In three colonies (Au: about 700 adults; Litzldorf: about 45 adults; Beyharting: about 200 adults) I monitored the presence of the marked individuals one to four times a month between May and August. The other colonies were also visited at least once a month in order to detect movements of banded bats (Zahn 1995). I did not visit the colonies after cold or rainy nights to avoid counting during times when many bats do not return to their roost (Audet 1990, 1992). However, local showers may have influenced some colony members in some cases: In the study area near the Alps local and short thunderstorms occur frequently in summer. Even when no rain was observed at the colony sites during the night, some bats may be prevented from returning to the roost by showers in the foraging areas, which can be located more than 15 km from the roosts (Güttinger 1994).

Banding of bats started during two previous studies, conducted in the same area between 1987 and 1990 (Audet 1992; Vogel pers. comm), when 214 females were marked in the colonies at Au and Litzldorf. In August 1991 I banded a further 116 young females in the colony of Au, 53 in the colony of Beyharting and another 52 females (adult and subadult) at male roosts in the study area (Zahn 1995). Each bat was banded with an aluminium ring (Zool. Museum Bonn). I fixed coloured spots of reflective tape to the aluminium rings to identify the bats over a distance of about two meters. Bats banded in the previous studies with plastic rings, could be identified over a distance of about 3 meters.

It was not possible to identify and to count all the banded individuals in a colony at

every visit, due to the density of the clusters and the bats' occasional use of alternative, partly hidden roosts at cooler places in the attics during hot weather. In the colony of Au, so many bats had been banded that it was not possible to identify all marked bats without disturbing the colony. Only the total number present was counted.

Definitions for each of the terms used in this study are given below.

Identified bats: the total number of banded females I located at a colony during one summer.

Maximum number of banded bats present: the maximum number of banded females which were present during a single visit to a colony

Average number of banded bats present: the average number of banded females at a colony (mean of all visits to a colony in one summer)

Average colony size: the average number of adult bats present in a colony in summer during periods of fine weather.

Maximum observed colony size: the maximum number of adult bats observed in a colony in summer.

Total colony size: the number of all adult bats living in a colony during summer.

Table 1 gives the number of the identified females in the colonies at Litzldorf and Beyharting and the presence of these individuals at the roost. The banded females observed in Au (where the bats could not be identified individually) are given in table 2. I never observed all identified bats of a colony at the same time at the roost. One year old females were absent from the colonies most frequently.

If all four samples of identified bats at least two years old (Beyharting and Litzldorf: 1993 and 1994) are summarised, on average 65% and at most 81% of those females were present when the counts were conducted (mean values of the four samples).

Table 1. Number of identified bats and their presence in the colonies of Beyharting and Litzldorf

colony	year	age of the bats (years)	IB (identified bats)	minimum presence (% of IB)	maximum presence (% of IB)	average presence (% of IB)	N (number of counts)
Beyharting	1992	1	13	31%	69%	57%	10
Beyharting	1993	2	11	27%	73%	59%	4
Beyharting	1994	3	7	14%	86%	61%	4
Litzldorf	1993	>2	15	53%	80%	68%	6
Litzldorf	1994	>3	12	58%	83%	72%	4

Table 2. Presence of banded bats in the colony of Au

colony	year	age of the bats (years)	MB (maximum number of presents bats)	minimum presence (% of MB)	average presence (% of MB)	N (number of counts)
Au	1992	1	48	25%	58%	7
Au	1993	2	40	63%	83%	5
Au	1993	>2	37	68%	82%	6
Au	1994	>3	62	74%	91%	5

In these cases the average values are about 80% of the maximum number of banded bats present, which coincides roughly with the observations in Au, where 85% (mean of the three samples) of the maximum number of at least two years old bats were present on average.

Counts of *Myotis myotis* leaving their roost at dusk at the three study colonies were conducted on 3 to 6 evenings at each colony evenings during periods of fine weather between the end of May and the beginning of July. The average colony size of the 3 colonies was 92%, 92%, and 91% of the maximum observed colony size for Beyharting, Litzldorf, and Au, respectively.

This difference between the maximum and the average observed colony size can be compared to the difference between the average and the maximum presence of banded bats at the roosts: For bats at least two years old the average presence (mean of all 7 samples) is 83% of the maximum presence and for one year old bats the average presence is 70% of the maximum presence (mean of the two samples of young bats banded in Au and Beyharting). One year old females represent about 10–11% of the females living in a colony in summer (ZAHN 1995). Thus the average presence of banded bats of all ages is about 82% of the maximum number of bats. Therefore a difference of about 10% exists between the average number of banded bats present (82%) and the average colony sizes (91–92% of the maximum observed colony sizes) but this may be caused by the methodological problems mentioned below.

However, this comparison shows that there is a considerable difference between the average and the maximum number of bats present in a colony during times of fine weather.

The low average presence of one year old females at the study colonies may indicate that most of them are not reproductive. Only about 10% of the females studied by HORÁCEK (1885) gave birth during their first year of life. If most of the one year old individuals do not have to care for offspring they may spend the day at other roosts more often than reproductive females.

Regular counts of colony sizes by other authors also indicate that many bats frequently are missing in colonies in spite of fine weather. ROGÉE and LEHMAN (1994) report that colony sizes already decreased in June during years with a high juvenile mortality. They assume that females may have left the colony after their offspring had died. ROER (1988) presents data of a colony in the Eifel (Germany) which shows fluctuations up to about 30% during periods of warm weather. In 1991, AUDET (pers. com.) counted bats leaving the colony at Au at dusk 11 times during dry weather (6.6.–7.7). The average value was 91% of the maximum observed colony size.

Additionally my data indicate a difference between the maximum observed colony size and the total number of females living in a colony: It never happened that all banded individuals were present in a colony at the same time (maximum number of bats present in a colony < number of identified bats). During most visits more than a quarter of the banded bats were not observed in the study colonies.

However, it is difficult to apply this figure to other colonies because of several methodological problems. In Au, where the sample size was high, the bats were not identified individually. Thus I could not prove whether the maximum number of banded bats present was lower than the number of banded individuals that lived in the colony, as is the case for Beyharting and Litzldorf.

Additionally, the counting in Au was diffcult as a consequence of the large size of the colony and the large number of banded bats. In Beyharting and Litzldorf the sample sizes were very small. Furthermore, if identified bats had died in summer they might have been regarded as missing for the rest of the season. Such mortality may have increased the difference between the number of identified bats and bats present.

In conclusion I recommend that future investigations on larger samples of *Myotis myotis* should examine the percentage of daily missing bats to allow more exact determinations of total colony sizes and population densities.

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Some notes on *Crateromys heaneyi* Gonzales and Kennedy, 1996 (Rodentia: Muridae) of Panay, Philippines

By R. Schweigert

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During a field survey on the island of Panay (West Visayas, Philippines) in October and November 1995, some additional results on the biology and distribution of the endemic *Crateromys heaneyi* (Panay cloud runner) were gathered.

The study site is located in the western province of Antique about 6 km east of the town of Culasi in the vicinity of Mt. Madja-as (2 090 m) and includes the areas around the villages Alojipan, Osorio and Flores at an altitude of about 100 m a.s.l. (Fig. 1). A description of the study area is given by Gonzales and Kennedy (1996).

Despite intensive searching only one family (two adults and two young) could be discovered in a tree hole. The author could not make direct observations nor estimations about the abundance of cloud runners. So it must be stressed, that virtually all given informations of this report (e. g. statements about nestconstruction and food plants) were gathered through interviews with local informants.

General descriptions and measurements of two adult *Crateromys heaneyi* males are available. The first specimen was caught during the survey described here in the Lewalew Creek, Baranggay Alojipan in the vicinity of Mt. Madja-as on 5. October 1995 at an altitute of about 100 m a.s.l. (Fig. 1). Head and body length was 25 cm, tail-length 28 cm, and length of hind foot 5.5 cm. Fur color was black, mottled gray in the rear. The nose and plantars were hairless and pink, the ears and eyes were black. The description of a second male from the Hamtang Forest (see below) is as follows (Curio pers. comm.): Head and body length 35 cm, tail length 34 cm, and weight 970 g. The fur color was black, mantle and face were gray. The belly was gray with a brown stripe. Plantars and nose were hairless and pink. The two individuals exhibit slight color variation as mentioned by Gonzales and Kennedy (1996). One scout reported, that there is a tendency in the fur of older individuals to become gray.

Den sites of the mainly arboreal cloud runners were found in holes of old trees and inside big tree ferns (Cyatheaceae). But it was also reported to rest in holes in the ground (e. g. between tree roots). Altogether, 19 den sites were found in 11 tree species (plant names after Seidenschwarz 1994):

Bischofia javanica Bl.*, *Canarium asperum* Bth., *Citrus macrophylla* Wester*, *Ficus* (3 spp.), *Hydnocarpus heterophylla* Bl., *Leea* sp., *Mangifera indica* L.*, *Pterospermum diversifolium* Bl., *Ziziphus talanai* Merr.

Three dens comprised of a ball- or dome-shaped "nest bowl" of leaves and twigs built in densely foliated branches of tree species marked with (*) in the list above. One of these dens measured about 50 cm in diameter and had an entrance of 15 cm at one side. Unfortunately, the three "nest bowls" had already been deserted and started to decompose. All inspected sleeping sites were stuffed with different amounts of dried grass and

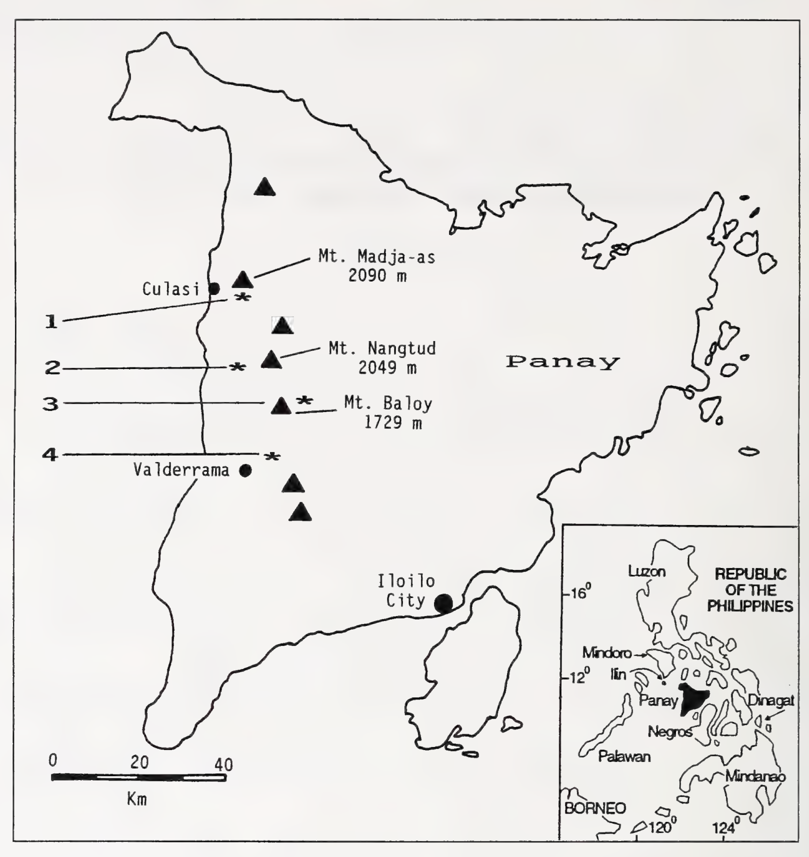


Fig. 1. Distribution of *Crateromys heaneyi* on Panay, Philippine Islands.
1) Confirmed record in the vicinity of the villages Alojipan, Osorio and Flores (see also Gonzales and Kennedy 1996); 2) Not confirmed record in the vicinity of Lumbuyan; 3) Confirmed record near Mt. Baloy (Terra typica) (Gonzales and Kennedy 1996; Oliver et al. 1993); 4) Confirmed record near Hamtang Forest (Curio pers. comm.)

shredded leaves of the supporting tree, that should have been collected by the Panay cloud runner.

On most occasions hunters have seen specimens inside their dens in groups of 2 (pairs) to 3 or 4 individuals (pairs with 1 and 2 young, respectivly). So it seems possible, that the young of a litter are reared jointly by female and male. Furthermore, it was reported, that families with young have been observed throughout the year.

The diet of the Panay cloud runner seems to be entirely vegetarian and consists of leaves, fruits, seeds, and roots of different plant species. Overall, 6 species of food plants were stated by informants (used parts in parantheses): *Garcinia linearifolia* Elm. (unknown), *Ficus* spec. (fruits), *Ipomea batatas* L. (roots), *Mangifera indica* L. (fruits), *Musa* spec. (fruits), *Psidium guayava* L. (fruits).

According to Gonzales and Kennedy (1996) *Crateromys heaneyi* is assumed to inhabit the whole Panay mountain range. During this survey the species was reported from the study site (see above) and the vicinity of Lambuyan, about 20 km south of Culasi. Curio (pers. comm.) reported on a male at the Hamtang Forest by the Sulud Bukidnon of Baranggay Nawili (Bugasong area, Valderrama) at an altitute of about 950 m a.s.l. in the south of the Panay mountain range on 22. March 1996 (Fig. 1).

Local people reported, that cloud runners are common in all locations mentioned were they live in altitudes up to 950 m a.s.l., but the results of this study suggest, that the density of the species is rather low.

Occasionally, specimens of *Crateromys heaneyi* are hunted by native people for food or for the pet market. There are different hunting-techniques. If the slow-moving animals walk on low branches, they are caught with a snare or pushed down with a stick and then seized on the ground. Sometimes, trained dogs are used to track down cloud runners. It was not possible to assess the hunting pressure by people or by feral dogs. But the latter seems to be responsible for the death of many individuals. During this survey, two Panay cloud runners were killed by dogs in a nearby village.

There are only few informations about cloud runners available, e. g. GONZALES and KENNEDY (1996), JONES (1982), MUSSER and GORDON (1981), MUSSER et al. (1985), NOWAK (1991), OLIVER et al. (1993), PASICOLAN (1993), RABOR (1986), and WIRTH (1990). GONZALES and KENNEDY (1996) and PASICOLAN (1993) studied the behaviour of *Crateromys heaneyi* and *Phloeomys pallidus*, respectively, in captivity. A comparison between their results and this study shows obvious similarities in the habits of both species. They are mainly nocturnal, use tree holes as den sites, and feed on vegetable matter. It is unknown whether *Phloeomys* also uses twig nests as does *Crateromys heaneyi*.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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MITTEILUNGEN DER GESELLSCHAFT

Wolf Herre

* 03. 05. 1909
† 12. 11. 1997



Am 12. November 1997 ist das Ehrenmitglied unserer Gesellschaft WOLF HERRE im Alter von 88 Jahren gestorben. Bis zu seinem Lebensende war er fröhlich, offen und voller Ideen; seine Mitmenschen und alle Ereignisse beobachtete er bis zuletzt mit kritischer, aber humorvoller Distanz.

WOLF HERRE wurde am 3. Mai 1909 in Halle/Saale geboren; seine Eltern waren der Baumeister KARL HERRE und seine Frau IDA. Am Reformrealgymnasium bestand er 1927 das Abitur; seinen Neigungen entsprechend begann er in Halle das Studium der Naturwissenschaften mit Schwerpunkt Biologie. Die sozialen Bedingungen in der Weimarer Republik waren schlecht; WOLF HERRE war gezwungen, Geld zu verdienen; er brachte es vom Hilfsarbeiter bis zum Hilfsschweißer und gewann dabei prägende Einblicke in das Leben von Handwerkern. Ersparnisse aus seiner Arbeit ermöglichten ihm 1929 einen Studienaufenthalt in Graz. Im Zoologischen Großpraktikum lernte er die „Wirbellosen" gründlich kennen. Graz war der Beginn langjähriger Freundschaften mit österreichischen Kollegen.

In Halle war inzwischen der gestrenge, aber um seine Studenten sehr bemühte Berthold Klatt Fachvertreter für Zoologie geworden. Er regte Wolf Herre nach dessen Rückkehr zu Arbeiten an Urodelen an. Die Themen waren: Strukturanalyse, Biologie, Systematik, Wirkung von Hypophysenhormonen, intraspezifische Variabilität. Wolf Herre wurde 1932 mit einer Dissertation über *Triturus cristatus* promoviert.

Damals gab es kaum Berufschancen in der Zoologie; Wolf Herre nahm deshalb eine Assistentenstelle im Institut für Tierzucht in Halle an, sicher ein Risiko für den Zoologen. Klatt aber hatte ihn auf Haustiere als interessante Objekte für die Zoologie aufmerksam gemacht. Die Tierzucht bot reichhaltiges Material und viele Anregungen zum Studium von Domestikationsfragen. Die Tierzucht nahm Gedanken und Ergebnisse zur Domestikation auf; in mehreren ihrer Hand- und Lehrbücher wurde das jeweilige einleitende Kapitel von Wolf Herre geschrieben.

Der Zoologie blieb Wolf Herre immer verbunden. Klatt ging 1934 nach Hamburg, Adolf Remane wurde sein Nachfolger in Halle. Remanes enorme Formenkenntnisse, seine klaren Formulierungen und Definitionen brachten Wolf Herre wertvolle Anregungen für die eigene Arbeit. Bei seinen Arbeiten über Urodelen hatte er sich mit fossilen Formen beschäftigt. Er gewann Kontakt zur Paläontologie, und mit einer Abhandlung über die eocänen Urodelen des Geiseltales habilitierte er sich 1935 für Zoologie und Vergleichende Anatomie. Bei seinen Darlegungen zur Stammesgeschichte der Urodelen bezog er auch Verhaltensmerkmale ein; heute spricht man von Evolutionsbiologie. Wolf Herre hat durch seine Zusammenarbeit mit der Paläontologie und Tierzucht schon damals interdisziplinäre Zusammenarbeit praktiziert, das sollte sich später noch erheblich verstärken. 1939 wurde er zum Diätendozenten am Zoologischen Institut Halle ernannt.

1939 erlebte Wolf Herre – wie die meisten seiner Generation – einschneidende Veränderungen, er mußte Soldat werden. 1940–41 durfte er noch einmal wissenschaftliche Arbeiten zum Abschluß bringen. 1941 heiratete er Dr. Ilse Rabes. 1942 wurde er zum apl. Professor ernannt; in diesem Jahr wurde er zum Fronteinsatz in Russland kommandiert. Durch „glückliche“ Umstände kam er gegen Kriegsende vom Baltikum nach Schleswig-Holstein, geriet dort in Gefangenschaft, aus der er bereits Ende 1945 entlassen wurde. Was tun, war die Frage.

Wolf Herre wandte sich an die Universität Kiel, die ihn als Hilfspräparator einstellte und noch Ende 1945 zum Diätendozenten ernannte. Da Remane seine Aufgaben als Institutsdirektor nicht wahrnehmen konnte, wurde Wolf Herre stellvertretender Leiter des Zoologischen Instituts und Museums. Die schwer zerstörte Universität Kiel erforderte einen Neuaufbau. Die besonderen Fähigkeiten von Wolf Herre gewannen nun Bedeutung: Organisationstalent, Begeisterungsfähigkeit und Optimismus. Trümmer wurden geräumt, Gebäude repariert, Kellerräume zu Labors umgestaltet, Sammlungsbestände gerettet. Das Zoologische Museum erfuhr eine Neugestaltung, und im Herbst 1946 folgte die Wiedereröffnung. Alle Arbeiten wurden von Professoren, Assistenten, Studenten, Mitarbeitern und Handwerkern gemeinsam geleistet. Dies bewirkte Zusammengehörigkeitsgefühl, Gestaltungswillen und eine positive Stimmung, die einmalig war. Die Stadt Kiel dankte Wolf Herre für den Wiederaufbau durch Verleihung einer Ehrenurkunde. All diese Aktivitäten erlaubten, daß der für die Kriegsgeneration so wichtige Studienbetrieb schon sehr früh nach Kriegsende in geordnete Bahnen gebracht werden konnte.

Adolf Remane konnte 1948 wieder die Leitung des Zoologischen Instituts übernehmen. Schon ab 1945 unterrichtete Wolf Herre Studenten der Landwirtschaft in Zoologie sowie Anatomie und Physiologie der Haustiere. Diese Aufgabe führte 1947 zur Gründung des Instituts für Haustierkunde; bis 1951 war es der Zoologie angegliedert. Einen Ruf nach Halle lehnte Wolf Herre 1949 ab; 1951 wurde er zum o. Professor für Anatomie und Physiologie der Haustiere sowie Zoologie ernannt. Die Haustierkunde war nun selbständig. Der Aufbau und die Gestaltung der Haustierkunde ist eine ganz persönliche Leistung von Wolf Herre; das Institut diente in Lehre und Forschung der Naturwis-

senschaftlichen und Landwirtschaftlichen Fakultät, es hatte eine Brückenfunktion. Nach einigen Jahren der räumlichen Enge und Improvisationen konnte 1959 ein Neubau mit Tiergarten bezogen werden.

Schon bald nach dem Kriegsende wurden Forschungsvorhaben begonnen, Haustiere und ihre wilden Verwandten rückten in den Vordergrund der Untersuchungen. Es ist schon erstaunlich, daß die von DARWIN so nachhaltig betriebene Domestikationsforschung erst wieder durch KLATT Beachtung fand und durch WOLF HERRE und seine Mitarbeiter intensiv vorangetrieben wurde. Die Domestikation führte für die Menschen zu einem fundamentalen Wandel der Lebensbedingungen. Zunächst waren zu klären: die Herkunft der Haustiere, der Vorgang der Domestikation und die Geschichte der einzelnen Haustierformen. Dies geschah in Zusammenarbeit mit der Vorgeschichte, der Archäologie und Kulturgeschichte. Für die Zoologie ist die Domestikation das größte Experiment mit Tieren; die Wirkungen dieses Experiments waren zu ermitteln. Es wurden Vergleiche der Stammarten mit ihren Haustieren angestellt. Diese Vergleiche erfolgten mit Methoden der Anatomie, Physiologie, Ethologie, Züchtungsbiologie und Allometrieforschung. Diese Untersuchungen wurden gefördert durch Zusammenarbeit mit den Grundlagenfächern der Human- und Tiermedizin und Tierzucht. Das große Bemühen um interdisziplinäre Zusammenarbeit wird deutlich durch WOLF HERRES jahrzehnte lange Freundschaft mit DIETRICH STARCK. Es stellte sich heraus, daß durch die Domestikation alle Organsysteme in Struktur und Leistung verändert worden sind. Weiterhin ist die Variabilität aller Merkmale bei Haustieren beträchtlich erhöht, was schon DARWIN als Argument für die Selektionstheorie diente. Domestikationsänderungen sind ausgesprochen auffällig und vielfältig; neue Arten aber sind im Hausstand nicht entstanden. Haustiere zeigen die vielfältigen genetischen Potenzen, welche innerhalb von Arten vorhanden sind. In der Domestikationsforschung sind noch viele Fragen offen; es ist zu wünschen, daß die wenigen Einrichtungen, welche sich mit der Haustierkunde beschäftigen nicht „Reformen“ zum Opfer fallen.

Die meisten Haustiere sind Säugetiere. Es ist also nur verständlich, daß sich WOLF HERRE in der Gesellschaft für Säugetierkunde engagierte; vor allem auch weil die Mitgliederzahl überschaubar ist und auf den Tagungen immer viele persönliche Kontakte und Gespräche möglich sind. WOLF HERRE war ab 1961 Mitherausgeber der Zeitschrift für Säugetierkunde. Er gründete die Schriftenreihe „Mammalia Depicta“, welche wir von 1966–1992 herausgeben konnten. Von 1962–1966 war er Präsident unserer Gesellschaft. 1958 und 1976 organisierte er unsere Jahrestagungen. Wissenschaftliche Gesellschaften sind auf Nachwuchs angewiesen. WOLF HERRE hat einen großen Teil des Unterrichts den Säugetieren gewidmet. Bei den Studenten waren die Exkursionen zu Museen, Zoologischen Gärten und Naturparks außerordentlich beliebt; viele wählten Examensarbeiten aus dem Gebiet Säugetiere und wurden Mitglieder unserer Gesellschaft.

Motivation zur Forschung war bei WOLF HERRE die Vielfältigkeit der Erscheinungsformen im Tierreich; diese wollte er verstehen, ihre Geschichte und biologische Bedeutung. Er hat die Probleme untersucht, welche seine Neugier fesselten. Er war in der Lage, bei der wissenschaftlichen Tätigkeit seine Unabhängigkeit zu bewahren. Seine Untersuchungen führte er durch im Labor, in Museen, Zoologischen Gärten und besonders in freier Wildbahn: 1942 Lappland, 1953 Anatolien, 1956/57 Südamerika, 1962/63 Afrika, 1962 Südamerika, 1971 Galapagos, 1972 Alaska und Japan. Die Reisen brachten wissenschaftliche Erkenntnisse, Erlebnisse, Abenteuer und sehr viel Ausbeute, die einer großen Zahl von Doktoranden als Untersuchungsmaterial diente und für manche Basis einer wissenschaftlichen Karriere wurde.

Die Themen und die benutzten Methoden der vielen Examensarbeiten waren entsprechend der Gesamtproblematik im Institut für Haustierkunde weit gefächert und reichten über die Domestikationsfrage hinaus in die Allgemeine Zoologie und in biologische Nachbarwissenschaften. HERRE-Schüler wurden Lehrer, Museums- und Zoodirektoren,

Paläozoologen, Protozoologen, Hirnforscher, Wildbiologen und Hochschullehrer in der Humananatomie, Humanphysiologie und Zoologie. Dies zeigt, daß eine fundierte biologische Grundausbildung die Fähigkeit zur Einarbeitung in verschiedene Spezialgebiete gewährleistet. Bei der Betreuung von Examensarbeiten hat sich WOLF HERRE größte Mühe gegeben, er kam aber nicht auf die Idee, bei Publikation solcher Arbeiten als Mitautor aufzutreten.

Ein ganz besonderes Anliegen war für WOLF HERRE die Schaffung von Publikationsmöglichkeiten, er war Mitherausgeber mehrerer Zoologischer Zeitschriften. Von 1948–1970 gab er die Verhandlungen der DZG heraus. Mit KOSSWIG, REISINGER und TUXEN gründete er die Zeitschrift für zoologische Systematik und Evolutionsforschung. Sein Grundprinzip als Herausgeber war die Bewahrung der freien Meinungsäußerung, er war gegen eine strenge Vorzensur, unterschiedliche Auffassungen sollten offen diskutiert werden. In diesem Sinne ist auch das von ihm und CURT KOSSWIG begründete Phylogenetische Symposium zu verstehen. Wissenschaftliche Qualität beurteilte er durch das Studium der Originalarbeiten, von den heute üblichen „Ranking-Methoden" hielt er gar nichts.

WOLF HERRE hielt es als Hochschullehrer für seine Pflicht, Aufgaben für die Gemeinschaft zu erfüllen. An der Christian-Albrechts-Universität übte er viele Ämter aus: 1951–1953 Dekan der Landwirtschaftlichen Fakultät, 1958–1959 Dekan der Naturwissenschaftlichen Fakultät, 1967–1968 Rektor der Universität. Von 1950–1970 war er Vorstandsmitglied der DZG. Durch öffentliche Vorträge hat er vielen Menschen Zoologie verständlich gemacht. Sein Einsatz erfuhr große Anerkennung: 1960 korrespondierendes Mitglied des Deutschen Archäologischen Instituts, 1964 Dr. h. c. der Medizinischen Fakultät Frankfurt, 1976 Ehrenmitglied der Deutschen Akademie der Naturforscher Leopoldina, 1979 Ehrenmitglied der Deutschen Zoologischen Gesellschaft, 1984 Ehrensenator der Universität Kiel.

WOLF HERRE war eine außergewöhnliche Persönlichkeit. Die Einheit von Forschung und Lehre und die zugehörige Freiheit, aber auch die dadurch resultierenden Pflichten für die Gesellschaft waren für ihn Gebot. Die Universität war für ihn kein Elfenbeinturm, er war weltoffen. Das Institut war für ihn auch ein soziales Gefüge, für alle Mitarbeiter war er immer zugängig als Ratgeber und Betreuer in ganz persönlichen Angelegenheiten.

Die Handlungen von WOLF HERRE waren bestimmt von Offenheit, Klarheit, Großzügigkeit und Entscheidungsfreudigkeit. Kontaktfreudigkeit und Humor zeichneten ihn aus. Er hatte viele Freunde. Den in jeder Beziehung überragenden Menschen gibt es nicht, auch WOLF HERRE hatte Ecken und Kanten; bei seinen vielfältigen Aktivitäten waren gelegentliche Auseinandersetzungen unvermeidlich. Streit aber hat er immer offen ausgetragen, damit klare Verhältnisse herrschten. Intrigen konnte er nicht leiden; erwischte er jemand bei einer Hinterhältigkeit, freute er sich „diebisch".

WOLF HERRE hatte ein langes erfülltes und ereignisreiches Leben; es ist zu wünschen, daß Persönlichkeiten wie er, auch in Zukunft an unseren Hohen Schulen tätig sein können.

M. RÖHRS, Hannover

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The New (XVIII) International Congress of Zoology

First Announcement

The date of the New Congress has been set for 4–9 September 2000 and the venue will be the Faculty of Philosophy, at the Universtity of Athens, Greece (under the auspices of the Hellenic Society of Zoology).

In order to reverse the present trend of fragmentation of Zoology and the crisis in the professional zoological education which became rampant after the suspension of the congresses in 1972, we have decided to dedicate this first renewed congress mainly to a number of integrative symposia and general discussions. We call upon you to participate!

Please inform us at the latest the end of September 1998 of your intention to participate and/or receive further information contained in our First Circular, contacting Dr. Rosa Polymeni, University of Athens, Department of Biology, Section of Zoology and Marine Biology, 15784, Athens, Greece., Tel. 30.1.7 26 43 64, Fax 30.1.7 28 46 04, e-mail:rpolyme@biology.db.uoa.gr

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Buchbesprechung

Klös, H.-G.: **Freundschaft mit Tieren.** Der Altdirektor des Zoologischen Gartens Berlin erzählt. Berlin: Edition q 1997. 347 S., 135 Fotos. DM 39,80. ISBN 3-86125-331-8

In zahlreichen Werken hat Hans-Georg Klös bezeugt, daß er ernste Sachverhalte mit lockerer Feder darzustellen vermag. Diese Fähigkeit macht auch das neue Werk zu einem interessanten, fröhlich lesbaren Buch. Klös gibt einen interessanten Einblick in seine Hilfsdienste als Schüler im Zoo Wuppertal, von seiner Tätigkeit als Student im Zirkus und seiner ersten Bewährung im Zoo Osnabrück. 1956 wurde ihm die verantwortungsvolle Aufgabe des Aufbaues und Ausbaues des Berliner Zoos anvertraut. Mit Schwung setzte er sich das Ziel, die Bebauung modern zu gestalten und einen vielfältigen Tierbestand zu gewinnen. Dazu waren Beziehungen weltweit aufzubauen. Reisen in unterschiedliche Gebiete waren geboten. Mit Unterstützung seiner Frau Ursula, die genaue Tagebücher führte, gelang es den Berliner Tierbestand einmalig auszubauen. Erlebnisse bei den weltweiten Reisen mit Tieren und Menschen gestatten eine bunte Schilderung, auch von der Geschichte und den Eigenarten der Länder sowie dem Leben der Tierarten in ihnen. Diese Vielseitigkeit macht das Lesen dieses Buches zu einer besonderen Freude.

W. Herre, Kiel

Instructions to Authors

Submission and Acceptance of Manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel, Germany, e-mail: dkruska@ifh.uni-kiel.de. Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by mail, and as soon as the peer reviews are received the authors will be informed concerning the decision for acceptance.

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Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.
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A new look at the identity and distribution of Water shrews (*Neomys* spp.) in Turkey

By B. Kryštufek, V. Vohralík, and C. Kurtonur

Slovene Museum of Natural History, Ljubljana, Slovenia; Charles University, Prague, Czech Republic; Trakya University, Edirne, Turkey

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Abstract

Examination of external, cranial, and penile characteristics of over 50 water shrews (*Neomys* spp.) from Turkey demonstrates the existence of two species. The smaller one, which is identical with *N. anomalus* Cabrera, 1907, occurs in both, European and the Asiatic Turkey, and is found from sea level to 2,100 m a.s.l. The larger species, previously ascribed to *N. fodiens* (Pennant, 1771), is reported here as *N. teres* Miller, 1908; *N. schelkovnikovi* Satunin, 1913 from the Caucasus is considered to be its junior synonym. *Neomys teres* occurs in the Pontic Mts. east of Bolu, and in the Van area. A single case of sympatric occurrence of the two species is reported from Lake Abant, north-western Anatolia.

Key words: *Neomys*, Turkey, distribution, nomenclature

Introduction

It is generally accepted that Turkey is inhabited by two species of water shrews of genus *Neomys: N. anomalus* Cabrera, 1907 and *N. fodiens* (Pennant, 1771) (Spitzenberger and Steiner 1962; Osborn 1965; Spitzenberger 1968; Kumerloeve 1975; Doğramaci 1989; Obuch 1994). In addition, Hutterer (1993) suggests that the Caucasian species *N. schelkovnikovi* Satunin, 1913 may also occur in Turkey.

The most comprehensive review of water shrew distributions in Turkey is that of Spitzenberger (1968). She reports *N. anomalus* in both European and Asiatic Turkey, but restricts *N. fodiens* to northeastern Anatolia – thirteen water shrew localities were known at that time. Since then, five mammal collecting trips to Turkey (1993 to 1995) have yielded new data which contribute further to our understanding of water shrew ranges and which have led us to new conclusions with regard to the identity of large Anatolian water shrews (thus far reported as *N. fodiens*).

Material and methods

Fourty-four specimens from seventeen different localities were collected by snap trapping or live trapping, using various trap types, often baited with a mixture of canned fish and oat flakes. Voucher specimens (skins, skulls, and phalli in 70% alcohol) are housed in the Department of Zoology, Charles University, Prague (PFUK) and in the collection of B. Kryštufek, Ljubljana (BKC). In addition, we reexamined Turkish specimens in the following collections (acronyms in brackets): Naturhistorisches Museum Wien, Vienna (NMW), Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK),

the collection of M. Çağlar, Istanbul University (ÇIU), and of J. Obuch, Blatnica, Slovakia (JOC). Details of the NMW and ZFMK specimens have been published by Spitzenberger (1968).

External measurements used in this study were taken from fresh specimens by two of the authors (BK and VV): W – weight, HB – head and body length (from snout to anus), TL – tail length (from anus to tail tip; hairs excluded), and HF – hind foot length (without claws). Ten linear measurements were taken from each skull, using a vernier calliper accurate to the nearest 0.05 mm: CbL – condylobasal length, RL – rostral length, RB – rostral breadth, BB – braincase breadth, IoB – infraorbital breadth, PB – breadth across pterygoid process, PgB – breadth across postglenoidal process, RH – rostral height, ML – mandible length, and CH – height of coronoid process. For definitions of RL, RH, and PB, see Tvrtković et al. (1980) (for the remaining measurements see Niethammer and Krapp 1990).

Morphometric dimensions were subjected to uni- and multivariate statistical analysis. Since our basic aim was the successful separation of taxa, stepwise discriminant function analysis (DFA) was used. This multivariate analysis identifies suitable linear combinations of the original variables that will allow the maximal possible separation between a priori defined groups (Manly 1994). Once the original groups are defined, DFA permits the classification of unknown specimen(s) into appropriate groups. Since DFA requires a priori defined groups, 43 specimens were ascried to 3 Operational Taxonomic Units (OTUs): OTU1 – *N. anomalus* from Turkish Thrace, OTU2 – *N. anomalus* from Anatolia (excluding sample from Lake Eber), and OTU3 – *N. teres.* Statistical analysis were undertaken using the STATISTICA analysis system (Release 5, StatSoft '97 Edition).

Results and discussion

Determination and identity of Turkish water shrews

The glans penis provides the most reliable discrimination between the three *Neomys* spp. currently recognised by Hutterer (1993): *N. anomalus*, *N. fodiens*, and *N. schelkovnikovi* (for the reasons explained below we henceforth use the name *N. teres* for the last). Particularly characteristic are the anterior part of the glans (short and blunt in *N. fodiens* and *N. anomalus*, elongated and narrow in *N. teres*) and the lateral flaps (absent in *N. anomalus*, present but small and simple in *N. fodiens*, much expanded and with horny spines in *N. teres*) (Pucek 1964; Yudin 1970). According to these criteria, the phalli of our specimens are ascribable either to *N. anomalus* (European and Asiatic material) or to *N. teres* (Asia Minor). *Neomys fodiens* was not represented in our material, although this could be an artefact of the limited number of phalli examined (n = 10). However, molecular data and skull shape analysis also suggest the presence of only two species of water shrew in Turkey, none of which is identical with *N. fodiens.*

Since the majority of voucher specimens in different collections are skins and skulls (and lack phalli) we attempt here to provide simple morphological (and particularly, cranial) characteristics that can be used to distinguish between Turkish water shrews. Size, which is often used for this purpose (e.g. Spitzenberger 1990 a) shows geographic variation in *N. anomalus* (Spitzenberger 1990 b). Furthermore, in the case of sympatry with *N. fodiens*, the size of two species can covary (Spitzenberger 1980) which makes accurate determination even more difficult, particularly when examining unprovenanced material.

Cranial characteristics permitting discrimination between Balkan populations of *N. fodiens* and *N. anomalus* are listed by Tvrtković et al. (1985), Kryštufek and Petkovski (1989), and Vohralík (1985). Our water shrews from European Turkey fitted fairly well with *N. anomalus* from Macedonia (based on Kryštufek and Petkovski 1989 and unpublished data by BK) but attain larger sizes and partially overlap with Macedonian *N. fodiens* (Fig. 1). Since *N. anomalus* is the only water shrew in European Turkey, this might represent character release following niche release in the absence of the larger, more aquatic, *N. fodiens.*

The two species from Anatolia belong to two size classes – the larger one represents *N. teres*, and the smallest one, *N. anomalus.* Phenetic relations between the two are similar

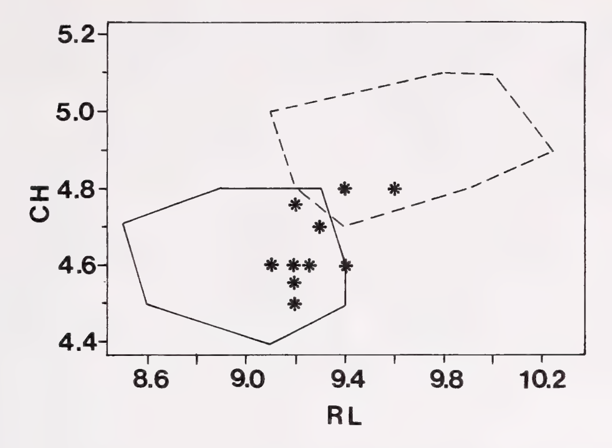


Fig. 1. Scatter diagram plot of coronoid height (CH) against rostral length (RL). Polygons enclose scores for 25 *Neomys fodiens* (broken line), and 28 *N. anomalus* (straight line) from Macedonia. Asterisks indicate specimens from European Turkey.

to those observed between *N. fodiens* and *N. anomalus* in Europe (SPITZENBERGER 1990 a). *Neomys teres* is more aquatic, with a longer tail and hind foot, and with more pronounced fringes of stiff hairs on the sides of the hind foot and along the ventral side of the tail. The skull lacked categoric traits, but several linear dimensions did not overlap, at least as long as the sample from Lake Eber was not considered. DFA of the three OTUs resulted in highly significant discrimination (Wilks' $\lambda = 0.0676$, $P < 0.0001$) and only single specimen of Thracian *N. anomalus* (OTU1) was mis-classified to OTU2. All *N. teres* were ascribed to the appropriate group. Six variables with F-to-enter >1 were included into the final model (Tab. 1). Two longitudinal measurements (CbL, RL), which seem to represent overall size, contributed most to between-group discrimination, and the 1st Discriminant function (explaining 93.5% of all discriminatory power) distinguished *N. teres* from both *N. anomalus* samples (Fig. 2).

Specimens from Lake Eber attain considerable size which makes their identity more equivocal. Although the only phallus available from the locality was of the "*anomalus*" type, several larger specimens suggest the possible co-occurence of *N. teres* in the sample. Since a discrimination model had been finalised and the discrimination functions had been derived, eight specimens from Lake Eber were examined for goodness-of-fit within the three OTUs. Six specimens (including the one with the "*anomalus*" phallus) had the highest posteriori probabilities ($P > 0.88$) for OTU1 (i.e. Anatolian *N. anomalus*), while the two largest specimens (CbL 21.3 and 21.8 mm, respectively) were classified as *N. teres*

Table 1. Summary of the Stepwise Discriminant Function Anaiysis of three Turkish *Neomys* OTUs. All F-values are significant at $P < 0.000001$.

Variable	Step	F-to-enter	λ	F-value
CbL	1	71.477	0.178	71.477
RL	2	5.315	0.132	26.352
PB	3	3.827	0.104	20.293
RB	4	2.693	0.087	16.690
PgB	5	2.009	0.076	14.188
IoB	6	1.608	0.068	12.329

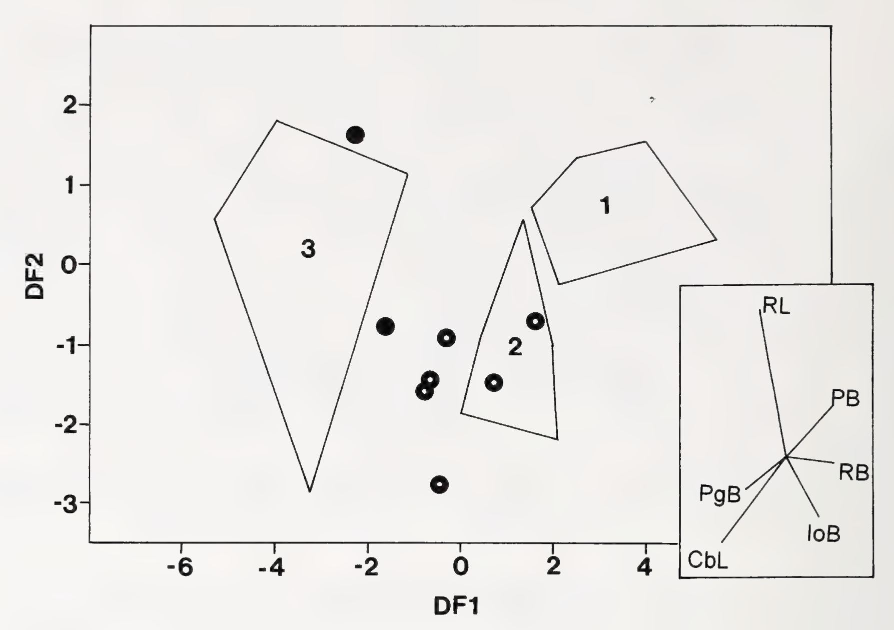


Fig. 2. Projection of three Operational Taxonomic Units (OTUs) of Turkish *Neomys* shrews onto the first two discriminant variates (DFs) derived from the stepwise DFA. Polygons enclose scores for all individuals within an OTU with identity numbers being placed on group centroids. Circles indicate specimens from Lake Eber (central Anatolia) which were superimposed onto the derived discriminant functions. Open circles = specimens with the highest posteriori probabilities for Anatolian *N. anomalus*; closed circles = specimens classified as *N. teres*. OTU1 = *N. anomalus* from Turkish Thrace (n = 10), OTU2 = *N. anomalus* from Anatolia (excluding sample from Lake Eber; n = 11), and OTU3 = *N. teres* (n = 14). The inset illustrates character vectors, based on their respective standardised coefficients for Canonical variables.

(posteriori probabilities 0.899 and 0.998, respectively). However, detailed examination of voucher skins of the two large water shrews showed no resemblance of the tail and hind foot to that of *N. teres*. Comparison of the Eber sample with *N. anomalus* and *N. teres* from lake Abant did not reveal such categoric external differences between large and the small size classes in the former as is evident between the two Anatolian species in Lake Abant (where they are sympatric). It is thus clear that the Lake Eber population belongs to *N. anomalus*. As a result, linear skull dimensions overlap to a certain degree between the two Anatolian water shrews, however, CbL, RL, and ML still permit fairly reliable discrimination (Tab. 2).

The first report on water shrew from Asia Minor is by Miller (1908). His specimen, collected from the vicinity of Erzeroum (= Erzurum; pt. 26 on Fig. 3) serves as the type for *Neomys teres*. There is no consensus on the identity of this name, it being synonymised either with *N. anomalus* (Ellerman and Morrison-Scott 1966; Gromov and Baranova 1981; Hutterer 1993) or *N. fodiens* (Spitzenberger and Steiner 1962; Corbet 1978). On the basis of size quoted from Miller (1908) (CbL = 22.4 mm) this specimen is referable to *N. schelkovnikovi*. It clearly represents the oldest name for a large water shrew from Asia Minor and the Caucasus; *Neomys schelkovnikovi* is thus a junior synonym of *N. teres*.

Distribution

Water shrews are reported from 31 localities; 6 are from European Turkey and the remaining 25 from Asiatic Turkey. *Neomys anomalus* is the only water shrew in European

Table 2. Summary statistics (upper row: mean ± standard deviation; lower row: range) and One way ANOVA of the external and craniometric measurements within 3 samples of Turkish *Neomys* shrews. See text for identities of morphometric characters. Weight is in grams, other linear measurements in mm.

	1 *N. anomalus* Thrace N = 10	2 *N. anomalus* Anatolia N = 17–21	3 *N. teres* Anatolia N = 11–20	F-value P <	Multiple range test
W	12.47 ± 4.007 7–20	12.74 ± 2.605 10–18	18.00 ± 5.979 11–28	6.456 0.005	(1, 2) (3)
HB	82.3 ± 5.186 74–89	82.5 ± 4.174 76–90	92.91 ± 7.314 85–101	15.151 0.0001	(1, 2) (3)
TL	51.90 ± 0.830 14.8–17.8	55.05 ± 4.143 46–60	67.75 ± 5.065 57–73	51.249 0.0001	(1, 2) (3)
HF	15.90 ± 0.830 14.8–17.8	16.70 ± 0.709 15.5–18.3	16.93 ± 1.143 18.2–22.1	59.678 0.0001	(1) (2) (3)
CbL	20.22 ± 0.392 19.35–20.85	20.97 ± 0.453 20.10–21.80	22.15 ± 0.436 21.60–23.00	63.991 0.0001	(1) (2) (3)
RL	9.23 ± 0.235 9.10–9.65	9.41 ± 0.242 9.00–9.95	10.12 ± 0.295 9.55–10.60	51.797 0.0001	(1, 2) (3)
RB	5.99 ± 0.219 5.05–6.20	6.04 ± 0.168 5.80–6.35	6.10 ± 0.162 5.70–6.40	1.452 n.s.	
BB	10.27 ± 0.296 9.65–10.65	10.46 ± 0.284 9.90–11.10	11.05 ± 0.379 10.40–11.75	20.870 0.0001	(1, 2) (3)
IoB	3.58 ± 0.178 3.30–3.80	3.67 ± 0.123 3.50–3.85	3.71 ± 0.136 3.40–3.90	2.990 n.s.	
PB	2.92 ± 0.102 2,75–3.05	2.80 ± 0.089 2.55–2.90	2.78 ± 0.139 2.50–2.95	5.321 0.01	(1) (2, 3)
PgB	6.11 ± 0.166 5.70–6.30	6.20 ± 0.137 5.90–6.45	6.37 ± 0.170 6.10–6.70	9.635 0.0005	(1, 2) (3)
RH	3.75 ± 0.123 3.50–4.00	3.83 ± 0.119 3.60–4.00	3.87 ± 0.171 3.60–4.20	1.284 n.s.	
ML	10.89 ± 0.423 9.85–11.45	11.21 ± 0.264 10.75–11.70	11.93 ± 0.238 11.60–12.50	52.502 0.0001	(1) (2) (3)
CH	4.64 ± 0.123 4.45–4.80	4.75 ± 0.150 4.40–5.00	4.87 ± 0.124 4.70–5.10	11.346 0.0001	(1) (2) (3)

Turkey (Fig. 3), where it ranges from sea level (pts. 4 and 5 on Fig. 3) to 650 m asl (pt. 2 b). Coastal records are from the Black Sea and Marmara Sea Coasts, and our specimens were collected along running waters (streams, rivers) in deciduous forest. This habitat is similar to that occupied by *N. fodiens* in much of Europe. The Anatolian range appears to be more scattered. The species occurs in the western-most Pontic Mts. (Kuzey Anadolu Dağlari) eastwards to the Yenice River in north-western (pts. 8 and 9) and central Anatolia (pt. 15), and in the Taurus Mts. (Toros Dağlari). Our results thus extend the known range of *N. anomalus* southwards by approximately 250 km.

Spitzenberger (1968) also reports *N. anomalus* for the Van area, which is separated from other Turkish localities by approximately 700 km. The voucher specimen on which the determination was based is stored in the ZFMK, and was examined by BK in December 1996. The skin, which is much contracted, does not permit any definite conclusion to be made about the species identity. The skull was not available for study at the time of

BK's visit to Bonn, however, Spitzenberger (1968) has published measurements for CbL and CH. Based on the former (20.6 mm) the specimen fits well with *N. anomalus*. Additional evidence on the occurrence of *N. anomalus* in eastern Anatolia emerged during a re-examining owl pellet material, previously identified as *N. fodiens* (Obuch 1994). The single right mandible from Sarikamiş (pt. 29 on Fig. 3) is small (ML = 11.3 mm) and fits

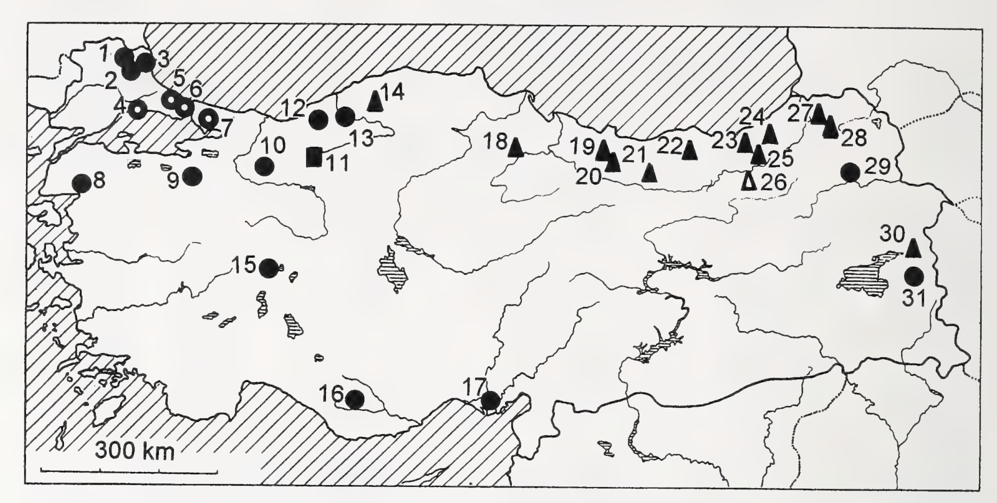


Fig. 3. Distribution of *Neomys* water shrews in Turkey. Circles = *Neomys anomalus*, triangles = *N. teres*, square = sympatric occurrence of the two. Filled symbols indicate specimens examined by BK.
List of localities includes exact location (including altitude if known), province of Turkey (villayet), and specimens examined (number, date, collection) (see text for collection abbreviations).
1 – Dupnisa Mağarasi, near Sarpdere (350 m), prov. Kirklareli (n = 2, 18 Oct. 1993, BKC); 2 a – Demirköy, prov. Kirklareli; 2 b – Velika Köprü, 12 km south-west of Demirköy (650 m), prov. Kirklareli (n = 8, 16–17 Oct. 1993, 22–23 June 1994, BKC and PFUK); 3 – Longoz (50 m), near Iğneada, prov. Kirklareli (n = 1, 3 July 1995, BKC); 4 – Paşa Alandere estuary (sea level), prov. Tekirdağ; 5 – Terkos Gölü (sea level), prov. Istanbul; 6 – Belgrad Orman, prov. Istanbul; 7 – Mahmutşevketpaşa, prov. Istanbul; 8–10 km south-east of Çirpilar, Kaz Mts., prov. Çanakkale (n = 1, 10 July 1995, PFUK); 9 – South-western slope of the Uludağ Mts., prov. Bursa (n = 1, 30 June 1994, PFUK); 10 – Hanyatak Köyü, Kapiorman Mts., prov. Sakarya (n = 1, 28 June 1994, BKC); 11 – Abant Gölü (950 m, 1 050 m), prov. Bolu (*N. anomalus* n = 2, 26–27 June 1994, BKC and PFUK; *N. teres* n = 3, 26 June 1994, BKC); 12 – Çayir, prov. Zonguldak (n = 2, 21 October 1993, BKC); 13 – 8 km north-west of Yenice (c. 100 m), prov. Zonguldak (n = 4, 2–3 July 1995, BKC and PFUK); 14 – 5 km north of Safranbolu (500 m), prov. Zonguldak (n = 1, 4 July 1994, PFUK); 15 – Doganköy, Eber Gölü (995 m), prov. Afyon (n = 8, 6 July 1995, BKC and PFUK); 16 – Balkusan (1 550 m), prov. Konya (n = 1, 12 Aug. 1993, PFUK); 17 – Yeşilobu (= Şahitlik, i.e. 15 km W of Adana) (24 m), prov. Adana (n = 1, 9 August 1969, ÇIU); 18 – 2 km east of Seyfe (c. 1 100 m), prov. Amasya (n = 1, 19 Sept. 1995, PFUK); 19 – Ulubey (800–1 100 m), prov. Ordu (n = 3, 20 May–2 June 1961 NMW); 20 – Topçam (850 m), prov. Ordu (n = 1, 21 June 1995, BKC); 21 – Tamdere (1 550 m), prov. Giresun (n = 4, 27 June 1995, BKC); 22 – Meryemana (1 000–1 300 m), prov. Trabzon (n = 1, 10 June 1961, NMW); 23 – Çamlik (1 380 m), prov. Rize (n = 1, 24 June 1995, BKC); 24 a – Çat (1 150–1 300 m), prov. Rize, 24 b – Ülkü (500 m), prov. Rize; 25 – Ovitdaği Geçidi, prov. Rize, 2 450 m (n = 1, 25 June 1995, BKC); 26 – 25 miles north of Erzurum (7 000 ft), prov. Erzurum, (type of *N. teres*, obtained on 8 July 1905); 27 – Kutul (2 200–2 400 m), prov. Artvin (n = 5, 17–18. July 1962, NMW); 28 – Yalnizçam-Geçidi (2 300–2 500 m), prov. Kars (n = 1, 7 August 1962, NMW); 29 – Sarikamiş (1 800 m), prov. Kars (n = 1, specimen from owll pellet, JOC); 30 – Bendimahi canyon, 5 km north-east of Muradiye (1 900 m), prov. Van (n = minimally 3 owl pellet specimens, JOC); 31 – Erçek Dağ (2 100 m), prov. Van (n = 1, 13 August 1935, ZFKM).
Corresponding references: Kahmann (1962) 6, 11 (*N. anomalus*); Miller (1908) 26; Obuch (1994) 29, 30; Osborn (1965) 7; Spitzenberger (1968) 2 a, 4, 5, 19, 22, 24 a, b, 27, 28, 31; Spitzenberger and Steiner (1962) 19, 22.

well with *N. anomalus*. Records of *N. anomalus* from eastern Turkey make Lay's (1967) statement of its occurrence on the Caspian coast of Iran (16 km ENE Goran) more likely also.

In Anatolia *N. anomalus* inhabits small brooks and rivers, occurring from the lowlands up to 2,100 m asl (on Erçek Dag; Spitzenberger 1968). The only central Anatolian record is from dense vegetation around Lake Eber (Eber Gölü). Specimens from southern Anatolia are from very different habitats: a garden at 45 m asl (near Adana) and dense vegetation along a stream in a karstic valley (Balkusan).

Neomys teres inhabits the Pontic Mts. as far west as Lake Abant, but the records became dense only to the east of Ordu. A single report from the Bendimahi Canyon, Van area, by Obuch (1994) and considered as *N. fodiens*, is based on 2 left and 3 right mandibles and one complete rostrum, all from owl pellets. Dimensions (ML: 11.7, 11.85, 11.9, 12.0, and 12.35 mm; RL 10.25 mm) strongly suggest *N. teres*. This record, being the only one outside the Pontic Mts., also speaks in favour on the occurrence of *N. teres* in Iran, as suggested by Hutterer (1993). All our *N. teres* specimens were taken along streams, mainly in mixed or coniferous forests, or from alpine meadows above the timber line. The altitudinal range encompassed was between 500 and 2,450 m asl.

The two water shrew species are mainly allopatric in Anatolia. *Neomys teres* was sympatric (but not syntopic) with *N. anomalus* in Lake Abant only (pt. 11), where the former occurred along a rapid mountain stream in a spruce (*Picea orientalis*) forest, approximately 100 m above the site where specimens of *N. anomalus* were obtained from a small river in mixed forest (950 m). Since *N. teres* is the only water shrew in the Caucasus (Sokolov and Tembotov 1989), Lake Abant appears to be the only locality known in which it occurs in sympatry with another *Neomys*.

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Zusammenfassung

Erneute Betrachtung der Identität und Verbreitung türkischer Wasserspitzmäuse (Neomys spp.)

Das Studium von Merkmalen der äußeren Gestalt, des Schädels und des Penis bei über 50 Wasserspitzmäusen (*Neomys* spp.) aus der Türkei belegt die Existenz von zwei Arten. Die kleinere, identisch mit *N. anomalus* Cabrera, 1907, kommt sowohl in der europäischen als auch in der asiatischen Türkei vom Meeresniveau bis zu 2 100 m Höhe vor. Die größere Art, bisher *N. fodiens* (Pennant, 1771) zugerechnet, wird hier als *N. teres* Miller, 1908 bestimmt, mit *N. schelkovnikovi* Satunin, 1913 aus dem Kaukasus als jüngerem Synonym. *Neomys teres* kommt im Pontischen Gebirge östlich von Bolu und im Gebiet des Van-Sees vor. Ein einzelner Fall von Syntopie der beiden Arten wurde am Abant-See in NW-Anatolien konstatiert.

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Variation and secondary sexual dimorphism of skeletal characters in *Glossophaga morenoi* and *G. leachii* from southwestern México (Chiroptera: Phyllostomidae)

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Abstract

Morphometric variation and secondary sexual dimorphism were evaluated and compared in 9 cranial and 23 postcranial characters of *Glossophaga leachii* and *G. morenoi.* Analysis of coefficients of variation (CV) showed that the degree of variation as well as its pattern are very similar for both species, with their CVs being lower than those found in birds and other mammals. Sexual dimorphism was tested using ANOVA and MANOVA. Results were significant for three cranial and three postcranial characters of *G. leachii*, as well as for nine postcranial traits of *G. morenoi.* Results of MANOVA on the same characters confirmed univariate results. Females are larger than males in most variables for both species, presumably as a result of higher energetic and physical demands of pregnant females and nursing mothers. Importance values in discriminating between sexes were calculated for each variable, importance profiles constructed, and significance of their correlations tested for cranial and postcranial characters separately to reassess the hypothesis that once differentiation occurs at the specific level, sexual dimorphism is no longer constrained in the same fashion as in the ancestral condition. Our results suggest that for cranial characters that is the case. For postcranial elements, however, importance profiles are highly correlated, suggesting that for characters with presumably higher fitness value, ancestral constraints remain after speciation has occurred.

Key words: *Glossophaga leachii*, *G. morenoi*, Dimorphism, morphometrics, skeleton

Introduction

Sexual dimorphism has been a matter of interest to biologists at least as far back as Darwin (1859). The mechanisms by which secondary sexual differences arise and are maintained within a population have been studied from the point of view of geneticists (Arnold 1985; Lande 1987), ecologists (Shine 1989), and systematists (Mayr 1942) alike. There has been an ongoing and yet unresolved controversy regarding which characters are selected to produce the dimorphic condition, and a number of hypotheses have been proposed (Selander 1966; Ralls 1976; Myers 1978; Shine 1989). Nevertheless, there seems to be consensus on the idea that maintenance of dimorphism is due, at least in part, to differential regulation of gene expression in males and females, and that it should be constrained within species inasmuch as genes are coadapted and characters involved are the product of pleiotropism (Lande 1987).

Consistent with this is the idea that populations within a species very likely would express sexual dimorphism via a consistent suit of morphometric characters because the

groups are linked to the degree to which they share gene pools (Willig and Hollander 1995). It is also possible, as these authors state, that although there may exist different balances among forces shaping dimorphism in each population, certain characteristics are more likely to change whereas others are more phylogenetically constrained. They also hypothesize that once speciation has occurred, coadapted gene complexes and genetic dynamics in general no longer constrain the expression of dimorphism, and that for the most part, patterns of intersexual variation are species-specific and relatively unrelated to systematic arrangements beyond the specific level.

Nectar-feeding bats of the genus *Glossophaga* are common in lowlands of Neotropical America (Webster 1993). Recently, large samples of *Glossophaga morenoi* and *G. leachii* were collected in southwestern México. Variation in *Glossophaga*, including sexual dimorphism, has been studied by Webster (1993), but his work was restricted to skull and external forearm and digit characters. This has been the case in most analyses of morphometric variation in bats (e.g. Power and Tamsitt 1973; McLellan 1984; Bogdanowicz 1992; Gannon et al. 1992), because mammals are traditionally kept as dried skins and skulls or the complete specimen is fixed in alcohol. From our samples, however, complete skeletons of all the specimens were available, allowing for the study and comparison of cranial and postcranial characters within each population. Species of the genus *Glossophaga* have gene pools that, although independent from each other, share a close common phylogenetic history. Similar patterns of sexual dimorphism are expected from them, with differences arising from differential selective pressures or distinct genome combinations inherited from their ancestral, common gene pool. Because both of the populations studied here were sampled in the same habitat type, variation due to ecological factors shaping particular characteristics of these organisms is assumed to be relatively constant.

The purpose of our study is to describe and compare the degree of intrapopulational variation within a sample of *G. leachii* and *G. morenoi*, with emphasis on secondary sexual dimorphism. We describe such differences from an univariate as well as a multivariate perspective, following the assertion of Willig et al. (1987) that, when analyzing large morphometric data sets in which characters are correlated, overall group differences are better evaluated by using multivariate techniques. Using the methodology developed by Willig and Hollander (1995), we assess the importance of particular characters in determining sexual dimorphism, and compare the expression of sexual differences between cranial and postcranial characters. Additionally, we reassess Willig and Hollander's (1995) hypothesis of relatively independent patterns of intersexual variation beyond the level of species.

Material and methods

Specimens were collected in two road culverts in southwestern México, 33 specimens of *G. leachii* in Oaxaca state (7 km N, 10 km E Tapanatepec, 730 m), and 40 of *G. morenoi* in Michoacán (22.2 km N, 7.0 km W Infiernillo, 350 m). Bats were caught in similar habitats, a scrub thorn-forest of *Prosopis* spp. and *Acacia* spp. (Rzedowski 1988). Four additional specimens of *G. morenoi*, collected about one kilometer apart from the culvert at Infiernillo, were also included in the latter sample. All specimens are adult (phalangeal epiphyses completely fused and cranial sutures well ossified), and were prepared as standard museum skeletons. Specimens are deposited in the osteological collection of the Subdirección de Laboratorios y Apoyo Académico (DP), Instituto Nacional de Antropología e Historia, México, D.F., México (*G. morenoi*: DP 6019–6021, 6817–6851; *G. leachii* DP 6465–6483).

A total of 9 cranial variables was measured following Webster (1993). Twenty-three postcranial characters were taken following López-González (1992). Measurements were taken to the nearest 0.1 mm using a digital caliper. All variables are greatest (maximum) lengths or widths. Their acronyms are as follow: length of the skull (GLS), condylobasal length (CBL), mastoid breadth (MAW), zygomatic breadth (ZYG), interorbital width (INT), length of maxillary toothrow (MAX), width across molars (WAM), depth of braincase (SKD), length of mandibular toothrow (MAN), length of first metacar-

pal (MCI), length of second metacarpal (MCII), length of third metacarpal (MCIII), length of fourth metacarpal (MCIV), length of fifth metacarpal (MCV), length of first phalanx of digit I (PlI), length of first phalanx of digit III (PlIII), length of second phalanx of digit III (P2III), length of first phalanx of digit IV (PlIV) length of first phalanx of digit V (P1V), length of radius (GLRA), length of humerus (GLHU), width of proximal epiphysis of humerus (GWPH), width of distal epiphysis of humerus (GWDH), length of the scapula (GLSC), width of the scapula (GWSC), height of atlas (GHAT), width of atlas (GWAT), length of innominate bone (GLPE), internal length of foramen obturatum (FORA), length of femur (GLFE), length of tibia (GLTI), length of fibula (GLFI).

To describe and compare the variation for each character within populations, coefficients of variation (CV) were determined for all of the variables in each population. In further analyses, measurements were transformed to their natural logarithms. Missing values were calculated by regressing each variable against the greatest length of the radius and substituting the estimated values for the missing ones. Secondary sexual dimorphism was tested for each character within each species using univariate analyses of variance (ANOVA). Multivariate differences between sexes were tested using MANOVA. Step-wise discriminant function analyses were performed to obtain linear combinations of variables that best described the differences between groups (sexes). Importance values (I) for each variable were calculated using the formula given by Willig and Hollander (1995). Because this is a two-group analysis, the formula is simplified to the square of the Pearson's correlation between the discriminant-function score and the original value of each character for each individual. Results are expressed in bar diagrams (importance profiles), in which the height of the bar for a particular character is equal to its importance value. The degree of concordance between character suites, in terms of importance profiles of variables, was evaluated by calculating the Pearson's correlation of importance values for each character between groups. To allow for comparison, all tests were performed on cranial and postcranial characters separately. Analyses were conducted using the Statistical Analysis System (SAS Institute Inc. 1987).

Results and discussion

General variation

Coefficients of variation are very similar for the two species analyzed (Tab. 1). In both of them, the greatest length of the skull (GLS) showed the lowest CV, whereas the depth of braincase (SKD) in *G. leachii*, and the greatest width across molars (WAM) in *G. morenoi*, showed the highest. CV values for skull characters are near those reported by Webster (1993) for all the species of *Glossophaga.* He reports CVs less than 3.5 for most of the measurements. CVs for postcranial measurements of *Glossophaga morenoi* range from 2.31 for the greatest height of atlas (GHAT), to 6.51 for the greatest length of the fibula (GLFI) (Tab. 1). *G. leachii* presents a similar range of CVs, with the lower limit (2.11) given by the greatest width of the distal epiphysis of humerus (GWDH) and the upper one (7.95) by the internal length of the foramen obturatum (FORA). In both species, CVs of postcranial measurements fall slightly below the typical values found in mammals (Bader and Hall 1960) and are closer to those found in birds, organisms considered by these authors as much less variable than mammals.

For both species, when wing elements are considered in proximo-distal series, CVs progressively increase the more distally they are positioned (Tab. 2). Bader and Hall (1960) obtained similar results in *Myotis* for digits completely embedded in the flight membrane, and a random distribution of CVs for bones of digit I. They explained the increase in CV as a result of a progressive replacement of bone by unossified connective tissue, and considered this trend to be in direct association with the time of onset of osteogenesis. However, *G. morenoi* and *G. leachii* showed the same pattern also in digit I, which is not in close association with the flight membrane. Additionally, it has been observed in *G. morenoi* (López-González 1992) that elements of digit I complete fusion and ossification right after birth (enabling the immediate use of the thumbs by newborns for clinging to the mother), whereas the process is completed almost at adulthood for the

Table 1. Mean, standard deviation, and coefficient of variation for 32 skeletal variables of *G. leachii* (18 males, 15 females) and *G. morenoi* (24 males, 20 females). Upper row, males; lower row, females. Coefficients of variation are shown for both sexes together.

	G. leachii			*G. morenoi*		
CHAR.	MEAN	STD	CV	MEAN	STD	CV
Cranial						
GLS	20.65	0.33	1.57	21.25	0.31	1.64
	20.91	0.26		21.42	0.38	
CBL	19.25	0.35	1.71	20.25	0.32	1.82
	19.55	0.21		20.44	0.40	
MAW	9.18	0.20	2.08	8.74	0.18	1.86
	9.13	0.18		8.78	0.13	
ZYG	9.59	0.17	1.91	9.21	0.23	2.46
	9.52	0.19		9.18	0.21	
INT	4.51	0.11	2.22	4.56	0.13	2.67
	4.57	0.07		4.57	0.10	
MAX	6.96	0.21	2.96	7.31	0.14	2.39
	7.13	0.16		7.41	0.22	
WAM	5.59	0.13	2.38	5.60	0.14	2.94
	5.63	0.13		5.61	0.19	
SKD	7.34	0.18	3.41	6.97	0.15	2.44
	7.23	0.30		6.89	0.19	
MAN	7.37	0.18	2.37	7.76	0.14	2.35
	7.47	0.16		7.81	0.22	
Postcranial						
MCI	3.26	0.18	5.82	3.13	0.17	4.82
	3.32	0.19		3.16	0.13	
MCII	30.35	0.97	3.49	27.71	1.01	4.39
	30.91	1.13		28.12	1.35	
MCIII	35.63	0.85	2.81	33.06	0.99	3.33
	36.19	1.12		33.09	1.09	
MCIV	32.61	0.82	2.85	30.14	0.87	3.37
	32.95	1.05		30.80	1.01	
MCV	30.65	0.71	2.93	29.08	0.93	3.38
	31.37	0.97		29.82	0.88	
P1I	4.17	0.28	5.87	4.22	0.24	6.22
	4.26	0.19		4.35	0.27	
P1III	12.35	0.44	3.73	12.43	0.52	3.59
	12.53	0.49		12.51	0.36	
P2III	17.01	0.63	3.47	15.11	0.70	3.95
	16.91	0.54		15.24	0.42	
P1IV	9.97	0.34	3.53	9.64	0.32	3.36
	9.92	0.37		9.82	0.32	
P1V	8.71	0.37	4.96	8.68	0.32	3.29
	8.76	0.50		8.73	0.24	
GLRA	34.95	0.99	3.04	32.69	0.86	2.87
	35.63	1.07		33.25	0.90	
GLHU	21.62	0.56	2.99	20.33	0.51	2.57
	22.24	0.60		20.83	0.40	
GWPH	3.92	0.11	3.40	3.46	0.11	3.19
	3.96	0.16		3.51	0.11	
GWDH	3.79	0.08	2.11	3.55	0.08	2.41
	3.81	0.09		3.57	0.09	
GLSC	14.67	0.35	2.47	12.61	0.31	2.68
	14.75	0.38		12.65	0.23	

Table 1. (Continued)

	G. leachii			*G. morenoi*		
CHAR.	MEAN	STD	CV	MEAN	STD	CV
GWSC	6.35	0.18	2.76	5.67	0.17	2.85
	6.38	0.18		5.72	0.12	
GHAT	3.32	0.11	2.90	3.07	0.07	2.31
	3.35	0.07		3.04	0.06	
GWAT	6.12	0.19	3.06	5.76	0.18	3.25
	6.14	0.19		5.89	0.16	
GLPE	9.53	0.19	3.94	8.70	0.22	3.51
	10.10	0.32		9.06	0.22	
FORA	2.19	0.16	7.95	2.10	0.11	5.79
	2.27	0.19		2.15	0.14	
GLFE	13.42	0.42	3.01	12.61	0.36	3.48
	13.53	0.39		12.83	0.38	
GLTI	12.75	0.42	3.66	11.67	0.30	3.50
	12.95	0.51		11.98	0.37	
GLFI	8.44	0.50	5.90	7.89	0.53	6.51
	8.54	0.51		8.26	0.45	

Table 2. Coefficients of variation of the forelimb elements of *G. leachii* (upper rows) and *G. morenoi* (lower rows) arranged in proximo-distal series. More proximal elements to the left, more distal ones to the right. Second phalanges of digits IV and V were not considered.

GLHU	GLRA	MCI	P1I		Digit
2.99	3.04	5.82	5.86		I
2.57	2.87	4.82	6.22		
		MCII			
		3.49			II
		4.39			
		MCIII	P1III	P2III	
		2.81	3.73	3.47	III
		3.33	3.59	3.94	
		MCIV	P1IV		
		2.84	3.53		IV
		3.37	3.36		
		MCV	P1V		
		2.93	4.95		V
		3.38	3.29		

rest of the wing elements. Alternative explanations are yet to be investigated for this trend, which also has been observed in forelimbs and hindlimbs of birds (Bader and Hall 1960).

Coefficients of variation for the length of the femur and tibia (Tab. 1) are higher than those for humerus and radius in both species. Elements of the first digit of manus, those not directly associated to the flying membrane, show higher CVs than the homologous elements of the other digits, modified for flight. It is possible to speculate on the importance for survival of keeping a narrow span of variation in structures involved with lift and loading in a flying animal compared to other elements of the same organism; one would expect the former to be the more conservative, and therefore to show lower CVs. Such a trend, however, is not clear within species for the skeletal structures studied.

Sexual dimorphism

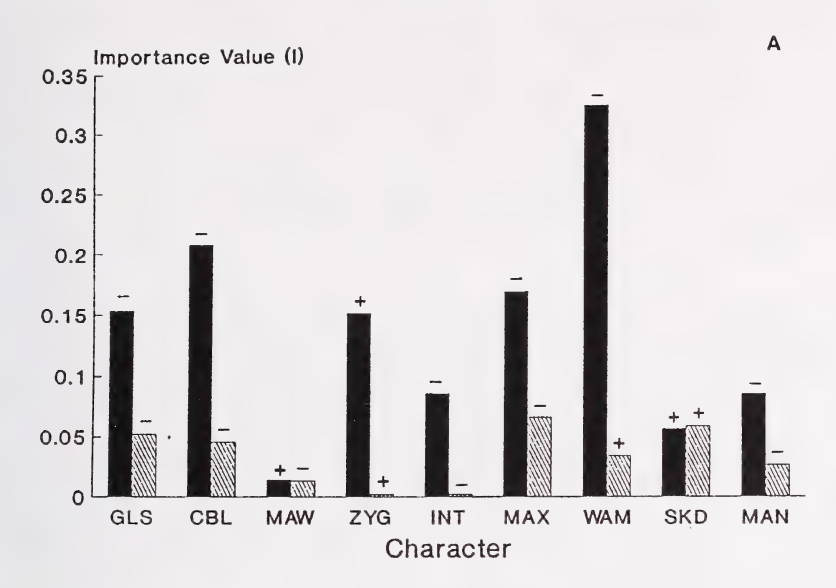
ANOVA was significant for three cranial variables in *G. leachii*. Coinciding with the univariate analyses, the result of the MANOVA was also significant (Tab. 3). In contrast, none of the cranial variables analyzed was significantly dimorphic for *G. morenoi*, and multivariate results were also nonsignificant. Importance profiles are different for each species (Fig. 1), which supports the idea that there is a species-specific pattern in the expression of sexual differences, as suggested by the results of ANOVA and MANOVA. This is further indicated by a nonsignificant correlation between importance profiles ($r = 0.6177$, $P = 0.0763$).

Results of postcranial comparisons, however, differ considerably from the cranial results. Nine variables were significantly dimorphic in *G. morenoi*, whereas only three were

Table 3. F-values and associated probabilities of ANOVA and MANOVA for sexual differences in 32 skeletal characters of *G. leachii* and *G. morenoi*. Asterisks indicate significance at $\alpha = 0.05$.

	G. leachii (N = 33)		*G. morenoi* (N = 44)	
VAR	F	P	F	P
Cranial				
GLS	5.71	0.023*	2.23	0.142
CBL	8.38	0.07*	1.93	0.172
MAW	0.41	0.528	0.64	0.429
ZYG	0.46	0.504	0.07	0.792
INT	3.04	0.091	0.09	0.760
MAX	6.44	0.016*	2.93	0.094
WAM	0.94	0.339	0.02	0.888
SKD	1.95	0.173	2.68	0.109
MAN	2.89	0.099	0.57	0.455
MANOVA	2.37	0.046*	0.87	0.555
Postcranial				
MCI	0.76	0.390	0.44	0.510
MCII	2.36	0.134	1.25	0.269
MCIII	2.61	0.116	7.07	0.011*
MCIV	1.03	0.318	5.25	0.027*
MCV	5.89	0.021*	7.09	0.011*
P1I	1.30	0.262	3.34	0.075
P1III	1.24	0.275	0.58	0.452
P2III	0.44	0.511	0.97	0.329
P1IV	0.21	0.647	3.36	0.074
P1V	0.08	0.780	0.38	0.541
GLRA	3.51	0.070	4.74	0.035*
GLHU	9.19	0.005*	11.98	0.001*
GWPH	0.43	0.515	1.99	0.166
GWDH	0.47	0.500	0.87	0.356
GLSC	0.39	0.539	0.23	0.636
GWSC	0.18	0.678	1.47	0.232
GHAT	0.66	0.423	1.17	0.285
GWAT	0.06	0.812	6.05	0.018*
GLPE	23.90	0.0001*	26.78	0.0001*
FORA	1.66	0.207	1.37	0.249
GLFE	0.57	0.456	3.89	0.055
GLTI	1.45	0.237	9.17	0.004*
GLFI	0.35	0.556	6.26	0.016*
MANOVA	1.59	0.238	2.36	0.028*

so for *G. leachii*. Results of MANOVA are in agreement with the univariate analyses, multivariate differences are not significant for *G. leachii* and significant for *G. morenoi*. Unlike in the skull, importance profiles of postcranial characters are highly correlated (r = 0.847, P = 0.0001). This is graphically evident also. Although importance values are different for each species, the patterns of the profiles are very similar (Fig. 1).



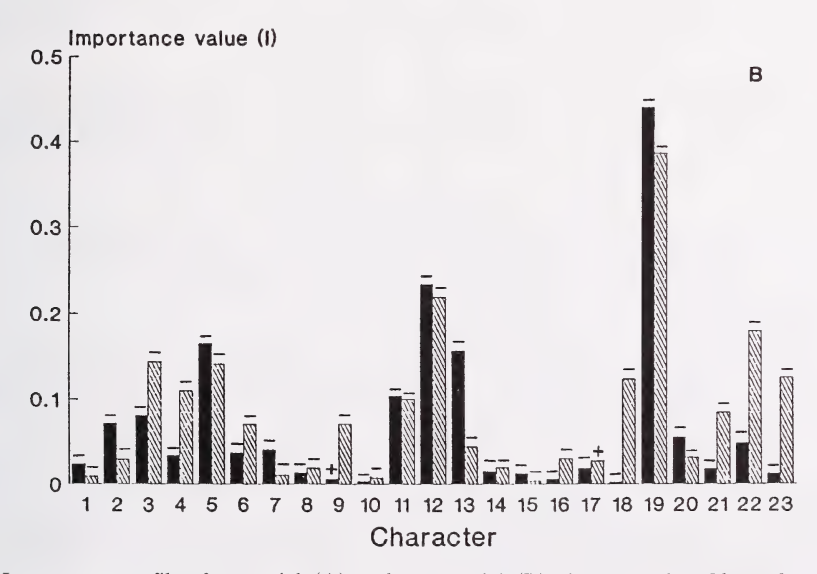


Fig. 1. Importance profiles for cranial (A) and postcranial (B) characters for *Glossophaga leachii* (black bars) and *G. morenoi* (hatched bars). Height of a bar for a given character estimates its relative importance in distinguishing between sexes. Females larger than males are indicated by a minus (–) on top of bar, males larger than females by a plus (+). Numbers in diagram B correspond to variables as follows: 1 = MCI , 2 = MCII, 3 = MCIII, 4 = MCIV, 5 = MCV, 6 = P1I, 7 = P1III, 8 = P2III, 9 = P1IV, 10 = P1V, 11 = GLRA, 12 = GLHU, 13 = GWPH, 14 = GWDH, 15 = GLSC, 16 = GWSC, 17 = GHAT, 18 = GWAT, 19 = GLPE, 20 = FORA, 21 = GLFE, 22 = GLTI, 23 = GLFI.

The variable with the higher importance value in both species is the length of the innominate bone. This is the skeletal structure where sexual dimorphism is most visually apparent in many mammals. In males of *Glossophaga*, the posteriormost part of the pubic bone bends medially to form a symphysis pubis. In females, it is directed backwards, resulting in a longer pelvis. The rest of elements that better describe sexual differences (those with the highest importance values) are directly involved with flight (MCIII, MCIV, MCV, GLRA, and GLHU) or with roosting (GLTI, GLFI) (Fig. 1).

Several hypotheses have been proposed to explain the origin and maintenance of sexual dimorphism. Competition among individuals of one sex, usually males, has been proposed as a selection process acting on morphological and behavioral traits (Trivers 1972). It has also been suggested that size differences between sexes may reduce competition for resources (Selander 1966). Myers' (1978) study on sexual dimorphism in vespertilionid bats showed that the degree of difference between males and females is greater for those species with greater fetal or neonatal weight, and that wing size of females is larger than that of males of comparable body size. He concluded that sexual dimorphism in those bats is influenced by demands of large fetuses. However, Williams and Findley (1979) considered that larger sizes of vespertilionid females are due to increased demands of energy during pregnancy, although they do not deny that weight loading may also be important. Ralls' (1976) hypothesis of the "big mother" proposes that a larger female would produce a larger baby with greater chances of survival because she could provide more or better milk, and could be better at carrying or defending her young.

Our data from the postcranial skeleton do not yield useful information to evaluate dimorphism as a result of sexual selection or competition for resources. They are, however, consistent with Myers' (1978) interpretation. Females are larger than males in those characters with high importance values, which are also associated with structures specifically involved in flying and roosting, rather than with general size. Considered as a whole, sexual differences found in the skeleton do not contradict Ralls' (1976) hypothesis either, and it is possible that being a "better mother" in these species has to do with her ability to carry and nourish large fetuses and young.

Regardless of the selective forces involved in maintaining these differences, our results also suggest that the skull, as a structure, is less constrained to change than the postcranial skeleton is. Willig and Hollander (1995) compared two populations of *G. soricina* from Brazilian caatinga and cerrado using cranial characters comparable to those of this study. Although they found significant differences between sexes in both sites, profiles of importance were not significantly correlated. Samples of *G. commissarisi* comparable to ours were analyzed by Webster (1993); he reported nonsignificant sexual differences for the variables measured.

Willig and Hollander (1995) hypothesized that legacy of gene pools in the past should limit the degree to which differences between sexes can be expressed in dimorphic taxa, and that correlations of profiles of importance values should decrease as comparisons are made at increasingly higher taxonomic levels. Using cranial characters, they found that most of their data did not correspond to this expectation. Thus, they concluded that once differentiation at the specific level occurs, expression of dimorphism is no longer constrained in the same way. Our cranial data are consistent with this conclusion, with the two species of *Glossophaga* differing in their expression of sexual dimorphism. They also differ with respect to the populations of *G. soricina* analyzed by Willig and Hollander (1995), and from those of *G. commissarisi* studied by Webster (1993).

In contrast, postcranial profiles show a high degree of coincidence. Even though for some characters sexes are not significantly different in *G. leachii* at the alpha level selected for this study (0.05), results suggest that sexual differences are expressed in a similar manner for this species and for *G. morenoi*. The postcranial profiles indicate that at least for these two species, the constraints to the expression of dimorphism from their

common ancestor remained in both taxa. Either there is a common selective force that keeps the patterns of variation between sexes constant, or speciation has taken place so recently that not enough time for significant changes has yet elapsed. The latter is more difficult to reconcile with what is observed in the skull, in which, apparently, differences between sexes are changing independently. A stronger selective constraint for each sex, at least in wing and hindlimb proportions, seems to be more likely, whereas for the skull, more plasticity is allowed. Patterns of intersexual variation may persist if the same selective pressures remain acting over the daughter species. Other characteristics, less constrained, will experience changes along their independent, new evolutionary pathways. This is consistent with our present knowledge of the genus *Glossophaga.* Although the characters that define the genus have been consistently understood and applied by most taxonomists, taxonomy within the genus has been rearranged several times during this century, mostly because of the high variability and overlapping of those skull characters used to distinguish among species (Webster and Jones 1980; Polaco and Muñiz-Martínez 1987).

Morphological variation is a reflection of the evolutionary factors that shape phenotypes. When comparing the two species studied, the general patterns of variation in terms of CV's are essentially the same for both of them. When patterns of sexual dimorphism are considered, our results suggest that the skull, as a structure, has been less constrained to change than the postcranial skeleton has. Apparently, after speciation occurred, selective pressures affected the studied populations differently, so that some parts of individuals have been more liable to change than others. Regardless of the selective force involved in maintaining secondary sexual differences, importance profiles for postcranial characters indicate that, at least for these two species, the constraints to the expression of dimorphism from their common ancestor remained in both taxa.

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Zusammenfassung

Unterschiede und sekundärer Sexualdimorphismus von Skeletmerkmalen bei Glossophaga morenoi und G. leachii des südwestlichen Mexiko (Chiroptera: Phyllostomidae)

Morphometrische Variabilität und sekundärer Sexualdimorphismus wurden in 9 cranialen und 23 postcranialen Merkmalen bei *Glossophaga leachii* und *G. morenoi* vergleichend untersucht. Eine Analyse der Variationskoeffizienten (VK) zeigte, daß das Ausmaß der Variation sowie dessen Struktur bei beiden Arten ähnlich war, mit einem geringeren VK als bei Vögeln und anderen Säugetieren. Sexualdimorphismus wurde mittels ANOVA und MANOVA untersucht. Drei craniale und drei postcraniale Merkmale zeigten sich signifikant bei *G. leachii* und neun postcraniale Charaktere bei *G. morenoi.* Eine MANOVA an diesen Merkmalen bestätigte die univariaten Ergebnisse. Bei beiden Arten waren die weiblichen Tiere in den meisten Variablen größer, wahrscheinlich adaptiv aufgrund höherer energetischer und physikalischer Anforderungen trächtiger Weibchen und säugender Mütter. Zur Trennung der Geschlechter wurden für jede Variable Gewichtungswerte berechnet. Gewichtungsprofile wurden daraus erstellt und die Signifikanz der Korrelationen zu cranialen and postcranialen Merkmalen separat getestet. Mit dieser Analyse wurde die Hypothese geprüft, daß bei einem bestimmten Differenzierungsgrad Sexualdimorphismus nich mehr in gleicher Weise bedingt wird wie in der evolutionär ursprünglichen Form. Unsere Daten legten nahe, daß dies bei Schädelmaßen in der Tat zutrifft. Bei postcranialen Merkmalen korrelieren die Gewichtungsprofile jedoch hoch signifikant, was darauf hindeutet, daß bei Merkmalen mit erwartet höherem Fitnesswert evolutionäre Zwänge nach erfolgter Arttrennung weiterbestehen.

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Biology of twinning and origin of an unusually high twinning rate in an insular mouflon population

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Abstract

Twins have rarely been reported from wild populations of European mouflons (*Ovis ammon musimon*), and this subspecies is commonly regarded as monotocous. During the winter of 1994, we autopsied 71 pregnant females in a population established on Île Haute, a small island of the subantarctic Kerguelen archipelago. Though pregnant yearlings always bore single fetuses, the twinning rate reached 36% among pregnant adult females. The study population was founded by two individuals, originating from the Vincennes Zoo (France). Our analysis of the birth registers revealed that multiple births were common in this zoo herd, and a founding effect may explain the high twinning rate observed during this study. Crossings with sheep (*O. ammon* f. aries) and oriental mouflons (*O. ammon orientalis*) during the recent history of the mouflon in continental Europe are probably responsible for the occurrence of twinning in the Kerguelen population, as well as in some captive mouflon populations.

Key words: *Ovis ammon musimon*, mouflon, reproduction, twins, Kerguelen

Introduction

Among Eurasian wild sheep (*Ovis ammon*), twinning is quite common in the Urial (i.e. *O. ammon orientalis*; Valdez 1976) and Argali groups (i.e. *O. ammon ammon*; Schaller 1977; Valdez 1988). In contrast, twinning is exceptional among American wild sheep (*O. nivicolla*, *O. dalli*, and *O. canadensis*; Spalding 1966; Geist 1971; Hoefs 1978; Eccles and Shackleton 1979). Twins are also uncommon among populations of European mouflons (*O. ammon musimon* Schreber, 1782): no multiple birth has been reported from the original populations of Corsica, Sardinia, and Cyprus (Pfeffer 1967), and their occurrence in most wild populations of continental Europe is much debated (Bon et al. 1991; Cugnasse et al. 1985). Females accompanied by two lambs were observed on some occasions, leading to speculations about the twinning ability of this subspecies (Cugnasse 1982; Bon et al. 1991). However, in ungulates, two or more young may temporarily associate with a female without implying kinship, and such reports are poor evidence of twinning. Even simultaneous nursings of two young are inconclusive: allosuckling has been reported in several ungulate species (Riedman 1982; Packer et al. 1992), notably in close relatives of mouflons, such as American wild sheep (Eccles and Shackleton 1979; Hass 1990) and domestic sheep (*Ovis ammon* f. aries; Poindron and Le Neindre 1980). This usually occurs while a female is already nursing her own single offspring (Murphey et al. 1995), a behaviour probably responsible for many unconfirmed field observations of twin-

ning among ungulates otherwise considered to be monotocous. The aims of this study are to investigate the biology of twinning in a population of European mouflons established on a small subantarctic island, and to compare their reproductive performances with those of the mouflon herd maintained at the Vincennes Zoo (France), from which the studied population derived.

Material and methods

The study was performed on île Haute (49°24′S, 69°56′E), a small island (6.5 km^2) of the Kerguelen archipelago. Details of the study area and climate have been reported elsewhere (Boussès et al. 1994). The vegetation is typically subantarctic and characterized by the absence of trees and shrubs. Rocky and eroded areas cover 70% of the island, while swards represent no more than 7%. The high population density during the study period must be considered in regard to these characteristics.

The study population was founded in 1957 by a pair of mouflons which came from the Vincennes Zoo (Lésel 1967). Following an initial period of rapid demographic growth, the Kerguelen population entered cyclic oscillations by the end of the 70's, with massive die-offs occurring every two to five years due to food shortages (Boussès et al. 1992). Our study was carried out from July to September 1994, during the austral winter, corresponding to the gestation period. The population density was very high, with about 100 ind./km^2, and a die-off occurred during the study period. Eighty females were shot and autopsied in the field. In this study, we have restricted the analysis to 71 females with embryos large enough to be detected macroscopically. The ovaries were bisected and examined for the presence of corpora lutea. Except for some ewes collected by hunters, the implantation side of embryos in the uterine horns was noted. Females were divided into yearlings and adults by the number of definite incisors (Ryder 1983).

Data on the reproductive characteristics of the founding stock were collected from the registers of births and deaths of the Vincennes Zoo. Although the zoo was created in 1934, complete registers are only available for the periods 1947–1965 and 1978–1988, and the origin of this collection is not reported. Unfortunately, mouflon multiple births were explicitely noted in very few cases. Two or more births were often recorded at a particular date, and multiple births were obviously much more frequent than those explicitely reported. However, the frequency of multiple reports provides only a crude estimate of multiple births since, for example, a double report might correspond to one set of twins or to two single-lamb births. Moreover, up to nine lambs were sometimes recorded the same day, and in several cases we suspect that the registration corresponds to a grouping of births for the preceding few days. To circumvent this problem, we examined for each year the ratio of the number of lamb births recorded to the number of potentially reproductive females present in the herd. Females were considered potentially reproductive at one year of age and able to give birth when 17 months old.

Results

In the Kerguelen population, twins were present in 33.8% of pregnant females (n = 71). The five yearling females sampled carried a single fetus, while 24 out of 66 (36.4%) pregnant adult females carried twins. There were 38 (53.5%) fetuses implanted in the right uterine horn and 33 in the left one, a proportion that did not differ significantly from a 50:50 distribution ($\lambda_1^2 = 0.553$, P = 0.55). The proportion of right-implanted embryos was similar for females with single fetus (51.5%, n = 33 fetuses) and those with twins (55.3%, n = 38; $\lambda_1^2 = 0.1$, P = 0.75). Among females with twins, the fetuses were always located in separate uterine horns when each ovary produced one egg (n = 6). In contrast, when the eggs were released by the same ovary, embryos shared the same uterine horn in only four out of 12 cases, a distribution explained by the trans-uterine migration of 33.3% of the eggs.

At the Vincennes Zoo, two pairs of twins and one set of triplets were explicitely recorded for 316 lambs born. However, only 57% of the reports referred unambigously to

Table 1. Distribution of birth reports at Vincennes zoo, according to the number of lambs noted on a particular date (periods 1947–1965, 1978–1988).

	Number of lambs per report									
	1	2	3	4	5	6	7	8	9	total
Number of reports	106	55	15	6	3	0	1	0	1	182
Proportion (%)	56.7	29.4	8	3.2	1.7	0	0.5	0	0.5	
Number of lambs	106	110	45	24	15	0	7	0	9	316
Proportion (%)	32.9	34.8	14.5	7.7	4.8	0	2.3	0	2.9	

Table 2. Reproductive characteristics of mouflons at Vincennes zoo, France, between 1949 and 1957. Though the potential number of reproductive females was known, the number of females failing to reproduce in any particular year was unknown, leading to minimal estimates of the number and proportion of twin-births

Year	Females	Lambs	Lambs/female	Min. number of twin births	Min. twinning rate
1949	13	15	1.15	2	0.15
1950	8	10	1.25	2	0.25
1951	15	17	1.13	2	0.13
1952	14	15	1.07	1	0.07
1953	12	18	1.50	6	0.50
1954	14	20	1.43	6	0.43
1955	15	23	1.53	8	0.53
1956	15	16	1.07	1	0.07
1957	18	16	0.89	0	0
total	124	150		28	
mean			1.23		0.23

single births (only one lamb recorded on a particular day), while double (29%) and triple daily reports of births (8%) were also frequent (Tab. 1). For a more precise analysis, we established the number of potentially reproductive females present each year from an analysis of the registers. Since we were interested in the characteristics of the herd before the founding of the Kerguelen population, we considered only the period 1949–1957. During this period, a mean number of 1.23 ± 0.22 (s.d., $n = 9$) lambs per potentially reproductive female was produced, and more than one lamb per female was evidently born in eight out of nine years (Tab. 2). Assuming that each potentially reproductive female reproduced, a minimum of 28 twin pairs is required to account for the excess of lambs produced. Thus, the twinning rate was at least 23% for the period considered, but exceeded 50% some years. These values are obviously underestimated, since some females could have failed to reproduce in a given year.

Discussion

In the île Haute population, females with twins always had two corpora lutea and the fetuses were located in separate embryonic membranes, indicating dizygotic twins. However, a female found dead in 1992 had two fetuses sharing the same embryonic membranes, a pattern that reveals the occasional occurrence of monozygotic twins (Renfree

1982). The predominance of dizygotic twins agrees with data on other ungulate species (Bazer et al. 1993).

As in most ungulates (Hafez 1993), eggs are produced equally by the two ovaries in mouflons. Twins tended to be implanted in separate uterine horns, even when the two eggs were produced by the same ovary. A trans-uterine migration of one egg occurred in these cases. We suggest that there is a selective advantage favoring this implantation pattern, which might result in reduced competition for resources between sibs. Indeed, it has been shown in several species that when the number of multiple fetuses differs between horns, those in the horn with a lower number tend to be heavier (Barr et al. 1970; Page et al. 1994).

All the yearling females autopsied in the Kerguelen population were pregnant but none had twins. Though based on a small sample (five individuals), this result agrees with those obtained for oriental mouflons in which reproductive yearling ewes always produce single lambs (Valdez 1976). It also conforms to most results for polytocous ungulates showing that primiparous females usually have a smaller litter size than older ones (e.g. Pimlott 1959 in moose *Alces alces*; Folk and Klimstra 1991 in white-tailed deer *Odocoileus virginianus*; Hewinson 1996 in roe deer *Capreolus capreolus*; Milner-Gulland 1994 in saiga *Saiga tatarica*; Clutton-Brock et al. 1991 in feralized domestic Soay sheep; Cassinello and Gomendio 1996 in Saharan arrui *Ammotragus lervia sahariensis*).

The twinning rate observed in the Kerguelen population is by far the highest reported for any mouflon population, with about 36% of the pregnant adult females bearing twins. One set of three male fetuses was even recorded for an adult female found dead during a winter die-off. In contrast, twinning is unknown in most free-living populations of continental Europe. For instance, all 51 pregnant females shot in the Caroux-Espinouse Massif, France, bore a single fetus (Cugnasse et al. 1985). When twinning occurs, it rarely exceeds a few percent of the births (1 to 3% in three populations studied by Briedermann 1992).

Multiple births have, however, been observed in several captive mouflon populations (Cugnasse et al. 1985). Twins represented 14% of births in an enclosed population in Germany (Briedermann 1992), approximately 10% of births at the London zoo (Zuckerman 1953) and at the New York Zoological Park (Crandal Lee 1964), and 5% at the National Zoo of South Africa (Brand 1963). The maintenance of a good food supply all year round may have contributed to the relatively high frequency of multiple births in captive populations. Ungulate fecundity is known to be very sensitive to diet quality (Sadleir 1969). For example, 22% of births involved twins in a captive population of Spanish ibex (*Capra pyrenaica*) with supplemented food, whereas no multiple births or females bearing two fetuses were observed in the founding population (Fandos 1989).

Improved food resources cannot, however, explain the twinning phenomenon observed in the Kerguelen population. During the study period, the population was at very high density and was obviously suffering from food shortage, as shown by the death of more than 50% of the individuals between June and November.

Our analysis of the Vincennes Zoo records revealed that twinning was very frequent in this herd. Thus, a founding effect is certainly responsible for the propensity of females to produce twins in the Kerguelen population. However, because twins are absent, or at least extremely rare, in the mouflon populations of the Mediterranean islands (Pfeffer 1967), the origin of this capability is probably linked to the recent history of the species. The introduction of mouflons in continental Europe can be traced back to the 18th century, and it is well established that some crossing occurred subsequently with domestic sheep and oriental mouflons (Pfeffer 1967; Uloth 1972). Some mouflon populations inherited the twinning capability from these crosses and the alleles responsible for this trait were surely introduced by chance into the Vincennes stock.

Inbreeding commonly results in substantial reduction in young survival, body size, and fecundity (Ralls et al. 1979; Falconner 1989). Since the Kerguelen population traces its

ancestry to only two individuals, we might have expected a reduced fecundity instead of the particularly high one observed. However, a history of forced inbreeding, as occurred in the Vincennes herd, may have purged the population of deleterious recessive alleles (SMITH 1978; LANDE and BARROWCLOUGH 1987). Indeed, there has been no external acquisition to the Vincennes Zoo population since 1947 at least, while the female population size varied between 8 and 19 individuals, and male number between only 4 and 9, such that the effective population size was extremely reduced.

Finally, our results bring a new insight into the population dynamics of the Kerguelen mouflon. LÉSEL (1969) first noticed that the population was characterized by a very high growth rate (46.3%) during the colonization period, a value much higher than those reported for other introduced mouflon populations. LÉSEL and DERENNE (1975) suggested that a highly-biased sex-ratio (i.e. 35 females for a total adult population estimated at 42 individuals in 1968) could account for the population growth rate. Present knowledge of the mechanisms controlling birth sex-ratio in ungulates is unable to explain such a huge excess of females (CLUTTON-BROCK and IASON 1986). The high fecundity revealed by this study offers a simpler explanation for the unusual growth rate observed.

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Zusammenfassung

Die Biologie von Zwillingsgeburten und mögliche Ursachen für eine ungewöhnlich hohe Rate von Zwillingsgeburten in einer inselbewohnenden Mufflonpopulation

Bisher wurde in freilebenden Mufflonpopulationen (*Ovis ammon musimon*) nur selten das Auftreten von Zwillingen beobachtet. Während des Winters von 1994 wurden in einer Population auf Île Haute, einer kleine Insel des subantarktischen Kerguelen-Archipels, 71 trächtige Weibchen autopsiert. Obwohl trächtige einjährige Weibchen stets nur einen Fötus aufwiesen, erreichte die Rate von Zwillingen bei den adulten Weibchen 36%. Die untersuchte Population geht auf zwei Gründerindividuen zurück, die aus dem Zoo von Vincennes (Frankreich) stammten. Eine Analyse des Geburtenbuches ergab, daß Zwillingsgeburten in diesem Zoobestand häufig auftraten, und die hohe Rate von Zwillingsgeburten in der Île Haute-population könnte daher auf einen Gründereffekt zurückgehen. Kreuzungen mit Schafen (*O. ammon* f. aries) und orientalischen Mufflons (*O. ammon orientalis*) während der jüngeren Geschichte des Mufflons auf dem europäischen Festland sind möglicherweise für das Auftreten von Zwillingsgeburten in Zoos und in der Kerguelen-Population verantwortlich.

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The House mice, *Mus musculus* s. l., hybrid zone of Transcaucasus

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Abstract

A description of the hybrid zone of house mice species of the Transcaucasus is given on the basis of allozymic data and morphological characters. It is demonstrated that the hybrid zone in the Transcaucasus is formed by three parapatric species: *M. musculus*, dwelling mainly in the north Caucasus; *M. domesticus*, inhabiting the area from western Transcaucasus to eastern Ciscaucasus; *M. praetextus*, widely represented in steppe regions of Azerbaijan. The main features of this hybrid zone are: (i) unusually high range of gene introgression throughout the entire Transcaucasus; (ii) a sharp boundary between *M. musculus* and the gene introgression zone between *M. musculus*, *M. domesticus*, and *M. praetextus*, stretching along the climatic boundary between continental and subtropical regions; (iii) the existence of a transitional zone in the Central Transcaucasus between *M. praetextus* and *M. domesticus*. The results obtained are discussed with regard to the hybrid zones of Europe and Eastern Asia. Two main features of Asian hybrid zones are emphasised: their unusually large width as compared to European examples and their localisation in climatic zones similar to the subtropics.

Key words: *Mus musculus*, hybrid zones, biochemical and morphological variation

Introduction

In recent years, the interest in the systematics of Palearctic representatives of the genus *Mus* has increased due to the introduction of biochemical systematic methods and the discovery of introgressive hybridisation between different forms (Selander et al. 1969; Selander 1970; Hunt and Selander 1971; Vanlerberghe et al. 1986, 1988; Nance et al. 1990), whose species status is discussed (Marshall 1986, 1991; Bonhomme 1986; Mezhzherin 1994).

Evidence obtained in Europe confirms the existence of a stable narrow hybrid zone between *M. musculus* and *M. domesticus*, several dozens kilometres wide, which passes throughout Europe, from Jutland across the Alps to the Balkans (Hunt and Selander 1973; Bonhomme et al. 1983; Kraft 1984; Vanlerberghe et al. 1986, 1988; Krystufek 1991). The geography of hybrid zones in Asia, where along with *M. musculus* Linnaeus, 1758, distributed virtually ubiquitously in the temperate and continental zone, there also occur southern species: *M. domesticus* Rutty, 1772, *M. praetextus* Brants, 1827 and *M. castaneus* Waterhouse 1843, which have received little attention. In addition to analysis of hybridisation between northern and southern species, it would be interesting to compare southern forms with one another, since the southern forms display considerable morphological differences (Marshall 1977) and they are also differentiated at the biochemical level (Sage 1981; Bonhomme et al. 1984).

A good possibility for analyses of hybrid zones of northern and southern species on the one hand, and European and Asian ones, on the other, is provided by the Caucasian region. In fact, this region combines the areas of three forms. *M. musculus* comes from the north, *M. domesticus* (syn. *M. m. formosovi* Heptner, 1930) penetrates from the south and the south-west, and *M. praetextus* from the south-east (Satunin 1905, 1909; Heptner 1930; Vereschagin 1957; Shidlovski 1947, 1958, 1976; Mezhzherin and Kotenkova 1989, 1992).

The main aim of the present study is the presentation of data on allozymic variability in house mice from the Caucasus; identification of morphological characters which appear to be diagnostic for *M. musculus, M. domesticus, M. praetextus* in this region; revision of museum collections on the basis of the distinctive features obtained; and, in the final analysis, specification of the range of these subspecies in the Caucasus.

Material and methods

Material

House mice from different regions of the Caucasus were analysed by method of protein and enzyme polyacrylamide gel-electrophoresis. Twelve specimens from Adjaria (Georgia), 8 house mice from Armenia, and 15 mice from Azerbaijan were investigated from the Transcaucasus region, 8 specimens from the Krasnodar region (Russia), and 7 from the Daghestan (Russia) in the Northern Caucasus region. Besides Caucasian mice, 3 individuals of *M. domesticus* from the Konstanz Lake region (Germany), 2 specimens of *M. praetextus* from Syria (type locality of this species), and 7 mice of *M. musculus* from Poland, and 112 from the Ukraine were examined as controls.

The house mice museum collections from the Caucasian region were investigated. The collections of the Zoological Institute of the Russian Academy of Sciences (N = 44), of the Moscow State University (N = 107), of the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine (N = 127), and of the Kiev State University (N = 35) were analysed. All Caucasian house mice samples are presented in figure 1.

Species diagnostics

Biochemical identification: Trapped mice were brought alive to the laboratory, where they were killed immediately before electrophoretic procedures. Diagnostics of *M. musculus, M. domesticus* species pair were carried out by identification of alleles at three biochemical loci (Es-1, Es-2, Idh-1). Identification of Transcaucasus house mice from representatives of *M. spicilegus* s. l. was performed by the following loci: Es-2, Es-15, Es-10, and Alb. Description of standard acrylamide electrophoresis methods and gel staining has been published earlier (Mezhzherin and Kotenkova 1992).

Morphological identification: Diagnostics of the pair *M. musculus, M. domesticus* of museum collections were performed by two well-known characters: belly colouration and relative length of tail and body (Orsini et al. 1983; Kraft 1984; Marshall 1986). For diagrams reflecting geographic variations of the mentioned morphological features, we used not less than three adult specimens for every record. Besides the above mentioned characters, we analysed the shape of the zygomatic plate and occlusal surface of the first lower molar, which have a diagnostic significance in identifications of *M. musculus, M. domesticus (*Orsini et al 1983; Kraft 1984; Kratochvil 1986).

The distinction of *M. musculus* s. l. from representatives of *M. spicilegus* s. l. was performed in the museum collections by the zygomatic coefficients (Orsini et al. 1983) and the relative length of the tail.

Results

Biochemical data

The frequencies of alleles of 28 loci of house mice from different regions are presented in table 1. Three reliable diagnostic loci for *M. musculus, M. domesticus* species have been

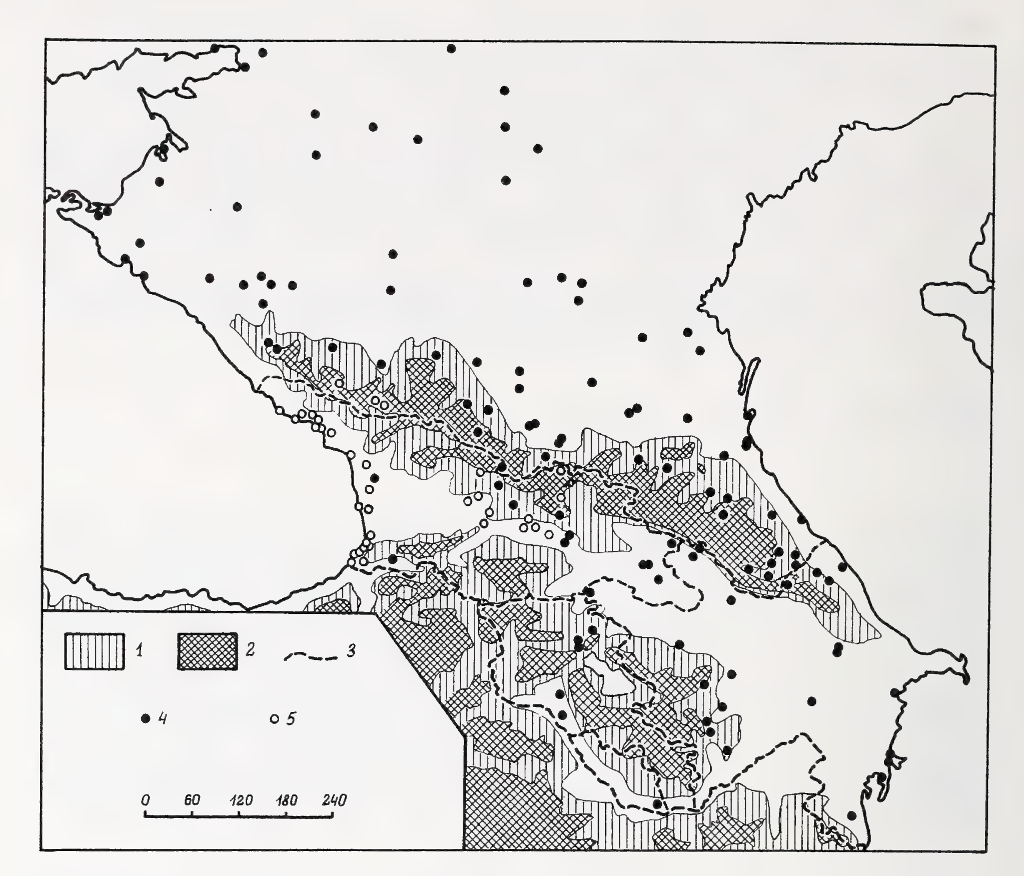


Fig. 1. Localities of house mice collection in Ciscaucasus and Transcaucasus. 1: highland from 1000 m to 2000 m above sea level; 2: highland more than 2000 m above sea level; 3: state borders; 4: localities of house mice collection in museums of Russia and the Ukraine; 5: localities of black-bellied mice collection (after: Shidlovski 1947, 1958).

found in this study corresponding to previous data (Selander et al. 1969; Thaler et al. 1981; Bonhomme et al. 1984).

Es-1: This locus is considered as diagnostic for *M. musculus*, *M. domesticus* after investigations performed in Europe (Selander et al. 1969; Selander 1971; Thaler et al. 1981; Bonhomme et al. 1984; Vanlerberghe et al. 1988). Among 290 individuals of *M. musculus*, which were investigated by the authors from the European part of the former USSR, Central Asia, and Siberia (Mezhzherin and Kotenkova 1989, 1992; Mezhzherin et al. 1992) and according to other data (Frisman et al. 1990), the Es-1^{100} allele was fixed. The slow allelic variant Es-1^{98}, which was fixed in *M. domesticus* and *M. spicilegus* s.l. (Thaler et al. 1981; Bonhomme et al. 1984), was revealed in two individuals from Central Asia (Mezhzherin and Kotenkova 1992). In the Transcaucasus region the allelic variant was predominant while in the mice of Adjaria it has been fixed (Fig. 2). The mean frequency of this allele in Transcaucasus house mice populations was 0.60 ± 0.04 ($t = 12.5$; $p < 0.001$) in contrast to the eastern Europe house mouse populations where allele Es-1^{98} was not found.

Es-2: This locus as well as Es-1 is traditionally used in the analysis of European hybrid zone (Selander et al. 1969; Selander 1971; Vanlerberghe et al. 1988), although the allelic variant intrinsic to *M. domesticus*, is always represented in *M. musculus* popula-

Table 1. Allelic frequencies of house mice species *Mus musculus* s. lato from different regions

Loci	Alleles	*musc.* Poland	*musc.* Ukraine	*musc.* Krasnodar region	*musc.* Daghestan	*praet.* Sirya	*praet.* Azerbaijan	*dom.* Adjaria	*dom.* Armenjia	*dom.* Germany
Aat-1	90						0.03		0.10	
	100	1.00	1.00	1.00	1.00	1.00	0.97	1.00	0.90	
Aat-2	–90	0.37	0.15							1.00
	–100	0.63	0.65	1.00	1.00	1.00	1.00	1.00	1.00	
Adh	–100	0.38	0.67	0.70	0.72	1.00	0.25	0.16	0.20	
	–105	0.62	0.33	0.30	0.28		0.75	0.84	0.80	1.00
Idh-1	95					1.00	0.19	0.50	0.52	
	100	1.00	1.00	1.00	1.00		0.81	0.50	0.48	1.00
Es-1	98					1.00	0.23	0.89	0.84	1.00
	100	1.00	1.00	1.00	1.00		0.77	0.11	0.16	
Es-2	null		0.23	0.25			0.21			
	100	1.00	0.66	0.75	0.58		0.37	0.03	0.52	
	103		0.11		0.42	1.00	0.52	0.97	0.48	1.00
Es-3	95		0.10							1.00
	100	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00	
Es-10	100	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00
	105							0.05		
Mod-1	98							0.04		
	100	0.50	0.79	0.67	0.76		0.84	0.80	0.50	
	101	0.50	0.18	0.33	0.24	1.00	0.16	0.16	0.50	1.00
	103		0.03							
Pgm-2	95	0.27	0.20	0.15	0.21		0.22		0.05	
	100	0.73	0.80	0.85	0.79	1.00	0.78	1.00	0.95	1.00
Sdh	100	1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	1.00
	101						0.06			
	105						0.06			
Hbb	d	0.44	0.57	0.55	0.46		0.50	0.20	0.15	
	p	0.28	0.13	0.45	0.54	1.00	0.50	0.19	0.35	
	s	0.28	0.30					0.61	0.50	1.00

Loci: Alb, Es-15, Es-9, Gdc-1, Gpd-x, Hba, Idh-2, Ldh-A, Ldh-B, Mor-1, Mor-2, Pgdh, Post, Sod-1, Sod-2, Tf were monomorphic under used electrophoretic conditions.

tions at low frequencies (Thaler et al. 1981; Bonhomme et al. 1984; Mezhzherin 1987; Mezhzherin and Kotenkova 1992; Frisman et al. 1990). In the Russian and Central *M. musculus* populations its frequencies do usually not exceed 10% (Mezhzherin and Kotenkova 1992; Frisman et al. 1990) while in Transcaucasus populations the allele predominates and in Adjaria it is even fixed (Fig. 3). The mean frequency of Es-2^{103} allele in Transcaucasus house mice was (0.657 ± 0.02) in comparison to investigated eastern Europe populations where its frequency was significantly lower (0.11 ± 0.007; $t = 25.0$; $p \ll 0.001$).

Idh-1: As well as the above-mentioned alleles, the slow migrating allele Idh-1^{95} is likewise characteristic for the southern house mice species (Asian populations of *M. domesticus*, *M. praetextus*, and *M. castaneus*, and representatives of *M. spicilegus* s.l.: Thaler et al. 1981; Bohhomme et al. 1984, 1989; Frisman et al. 1990; Britton-Davidian 1991). In the territory of the former USSR, in European, northern Caucasian, Middle-Asian, and Siberian house mice populations the slow migrating allele was never recorded (Mezhzherin 1987; Mezhzherin and Kotenkova 1989, 1992; Mezhzherin et al. 1992;

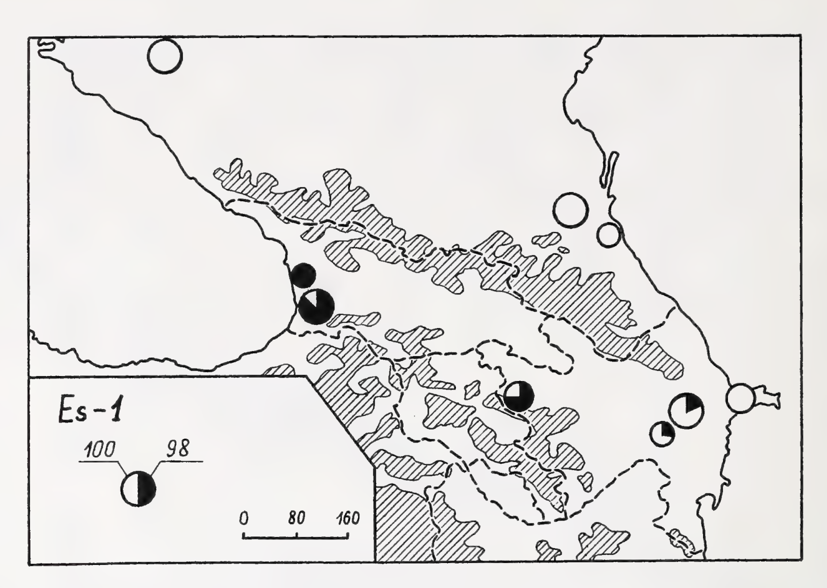


Fig. 2. Diagram of geographic distribution of Es-1 alleles in the Caucasus region. The scale of maps Figs. 2–6: 1 : 800 000; shaded areas are highland more than 2 000 m above sea level.

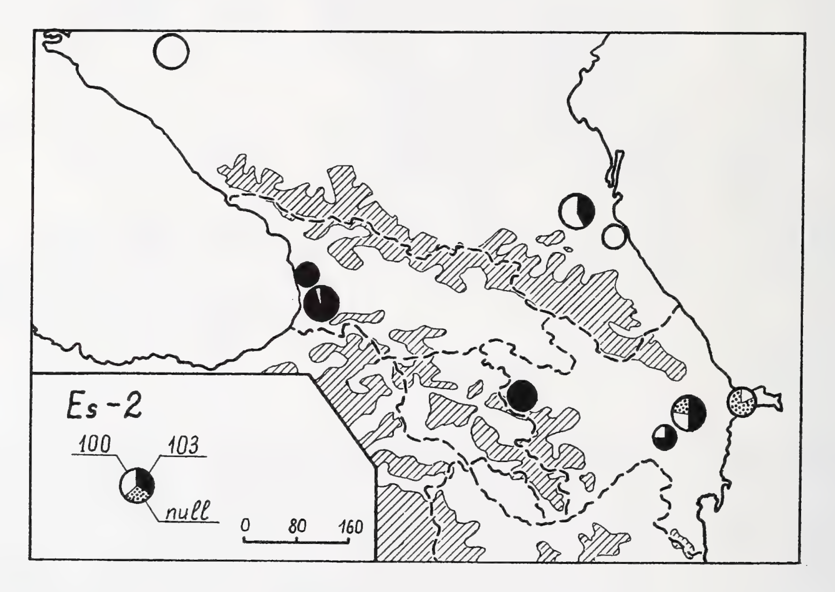


Fig. 3. Diagram of geographic distribution of three alleles of Es-2 locus in the Caucasus region.

Milishnikov et al. 1989, 1990; Frisman et al. 1990). The appearance of this allele was found only in the Transcaucasus (Fig. 4), where mean frequency was 0.371 ± 0.041 ($t = 9.04$; $p < 0.001$). In addition, this allele at high frequencies was found in the south of the Russian Far East (Frisman and Korobitsina 1990), where gene introgression took place from *M. castaneus* to *M. musculus.*

In addition to the alleles of the above-mentioned loci, the Transcaucasian house mice populations can be characterised by $Sod\text{-}1^a$, $Pgm\text{-}1^a$, $Gpd\text{-}1^a$ (Milishnikov et al. 1990;

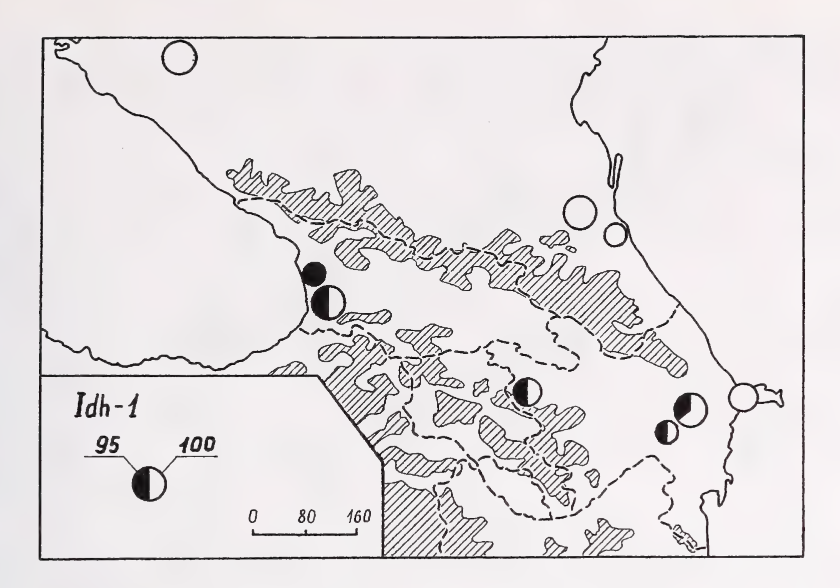


Fig. 4. Diagram of geographic distribution of two alleles of Idh-I locus in the Caucasus region.

FRISMAN et al. 1990), and Mod-2^a (MEZHZHERIN and KOTENKOVA 1992). In Transcaucasus populations they are met together with the Es-1^{98}, Es-2^{103}, and Idh-1^{95} proving the existance of *M. musculus* and *M. domesticus* gene introgression in this region.

Comparison of eastern Transcaucasus white-bellied *M. praetextus* with western dark-bellied *M. domesticus* yielded no considerable difference at the biochemical gene level, except for the Hbb locus. The allele Hbb^s, predominating in western European *M. domesticus* (BRITTON-DAVIDIAN 1989), is represented at a high frequency in the occidental Transcaucasus form also. Therefore, we suggest a direct relationship between the Transcaucasian *M. domesticus* populations and the European ones. Predominance of the Hbb^p and absence of Hbb^s in the oriental transcaucasus populations within white-bellied house mice indicate their Asian origin, where very similar gene distribution of Hbb locus is observed (MIYASHITA et al. 1985).

Morphological variation

Presence of at least two forms of house mice belonging to the species group *M. musculus* s. l. has been traditionally recognised in the Transcaucasus region (SATUNIN 1905, 1909; HEPTNER 1930; ARGIROPULO 1940; VERESTSCHAGIN 1959; SHIDLOVSKI 1947, 1958, 1976). They were the occidental dark-bellied mouse *M. m. formosovi* (syn. *M. domesticus*) and the oriental white bellied form identified by many authors as *M. m. praetextus*, *M. m. bactrianus*, *M. m. tataricus* (partim!). Revision of collections confirms this concept in general, although the pattern of variability of belly colouration has proven to be far more complicated (Fig. 5). Dark-bellied mice with no distinct belly and back colouration occur in the moist subtropics of Adjaria. In central Georgia and Armenia mostly dark-bellied specimens with distinct albino spots of diverse shape are distributed. In Daghestan, where *M. m. formosovi* was described, the most diversified colour variants of typical *M. musculus*, *M. domesticus*, and *M. praetextus* and their combinations occur. In steppe regions of central Azerbaijan exclusively white-bellied mice with a brown back are found (Fig. 5). These mice were recognised by SHIDLOVSKI (1976) as *M. m. praetextus.* External

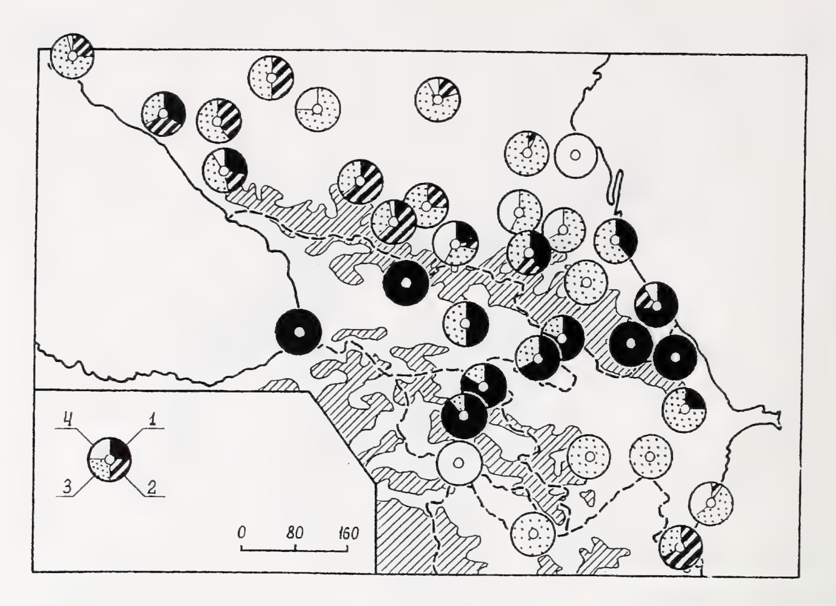


Fig. 5. Diagam of geographic distribution of different types of belly's colouration in the Caucasus region. 1: black belly mice; 2: dark-grey belly mice; 3: light grey belly mice; 4: white belly mice.

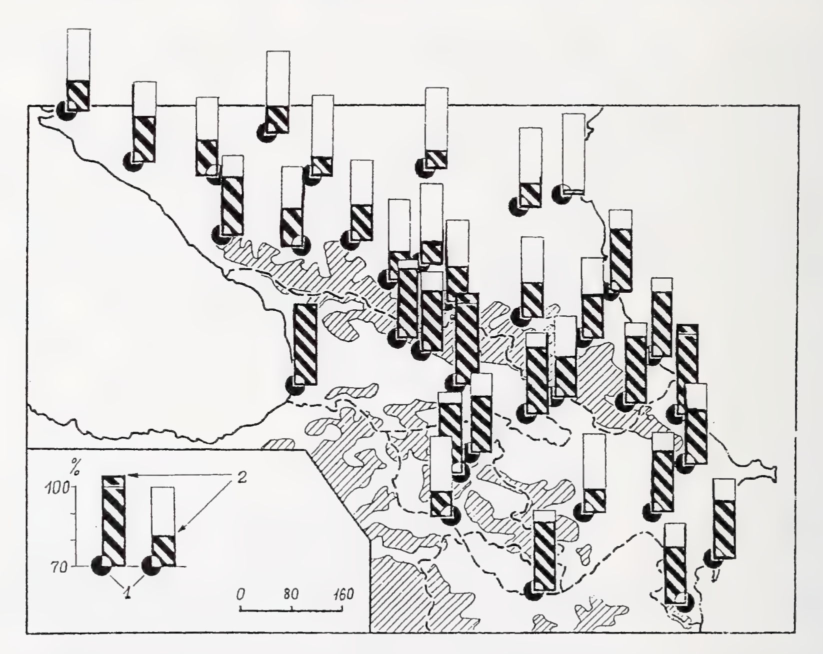


Fig. 6. Diagram of geographic distribution of house mice with different length of tail in the Caucasus region.

morphology of the house mice from Azerbaijan do not differ in appearance from those from Syria. These are large white-bellied mice with a tail equal or longer than body. The colouration on the back varies from sand-coloured to brown. In addition, on the edge of the distribution ranges of *M. domesticus* and *M. praetextus*, on the borders of Azerbaijan,

Georgia, and Armenia mostly grey-bellied mice occur. Their coloration contrasts with both dark-bellied occidental and white-bellied oriental forms. Most likely, they resulted from hybridisation between *M. domesticus* and *M. praetextus.*

The geographical variation of the relative tail length of the house mice of the Caucasus is presented in figure 6. Considerably long-tailed are mice from Transcaucasus and Daghestan, whose relative tail length varies within 90–110%. In the North Caucasus, in the regions of the Great Caucasus and the Black Sea coast, the tail is always shorter than the body (80–90%). In dry continental regions of the North Caucasus, and particularly in semideserts, mice have the shortest tails (70–80%).

Measurements of skull and body of the Cis- and Transcaucasus mice are given in table 2. Virtually all the measurements of the Ciscaucasian mice are smaller than those of the Transcaucasian ones. On this background considerable differences are found in the Transcaucasian population, too. House mice from the western Transcaucasus show a greater ear length and interorbital distance than those from the eastern Transcaucasus. In general, occidental specimens appear rougher than oriental *M. praetextus*, largely due to a thick tail and massive skull.

Table 2. Measurements of main characters of the skull and body in three house mice species

Characters	Species		
	M. musculus Northern Caucasus	*M. domesticus* Adjaria	*M. praetextus* Azerbaijan
Length of body (mm)	78.8 ± 1.11	81.7 ± 1.34	80.3 ± 1.15
Length of tail (mm)	64.4 ± 2.18	81.4 ± 2.24	75.0 ± 1.58
Length of foot (mm)	15.9 ± 0.11	16.9 ± 0.12	16.9 ± 0.10
Height of ear (mm)	13.0 ± 0.1	14.4 ± 0.14	13.8 ± 0.22
Relative length of tail (%)	82.0 ± 2.0	100.0 ± 3.10	93.0 ± 2.0
Condylobasal length (mm)	20.0 ± 0.16	20.7 ± 0.24	20.6 ± 0.19
Length of foramina incisiva (mm)	4.8 ± 0.08	4.9 ± 0.06	4.9 ± 0.08
Length of upper molars (mm)	3.2 ± 0.02	3.2 ± 0.02	3.3 ± 0.04
Infraorbital width (mm)	3.6 ± 0.05	3.7 ± 0.04	3.4 ± 0.03

The traditional shape of the masseteric plate is used as a diagnostic character of house mice species (Marshall 1977; Orsini et al. 1983; Kraft 1984; Kratochvil 1986). In the Central Asian house mice species *M. bactrianus* (= *M. praetextus*), the anterior edge of the plate is round, while specimens of *M. domesticus* have the shape of a protruding angle, and in *M. musculus* the anterior edge is slightly a rounded or angular in shape. A comparative analysis of this morphological characteristic of Transcaucasus house mice and *M. musculus* from North Caucasus and Ukraine, *M. domesticus* from Germany, and *M. praetextus* from Syria (Fig. 7) indicates that the western Transcaucasian mice have a masseteric plate most similar to that of European *M. domesticus.* House mice from eastern Transcaucasus have a rounded plate outline, similar in shape to that of *M. bactrianus* (= *M. praetextus*).

A notable morphological characteristic of *M. domesticus* is the pattern of an occlusal surface of the first lower molar (Orsini et al. 1983; Kraft 1984). Of all transcaucasian mice analysed by electrophoresis, only some individuals from Georgia demonstrated the occlusal surface of M_1, in shape similar to that of *M. domesticus* (Fig. 8). The remaider of the mice from the region shows patterns usual for *M. musculus.* The populations of *M. musculus* from the northern Caucasus demonstrate a pattern typical for this species.

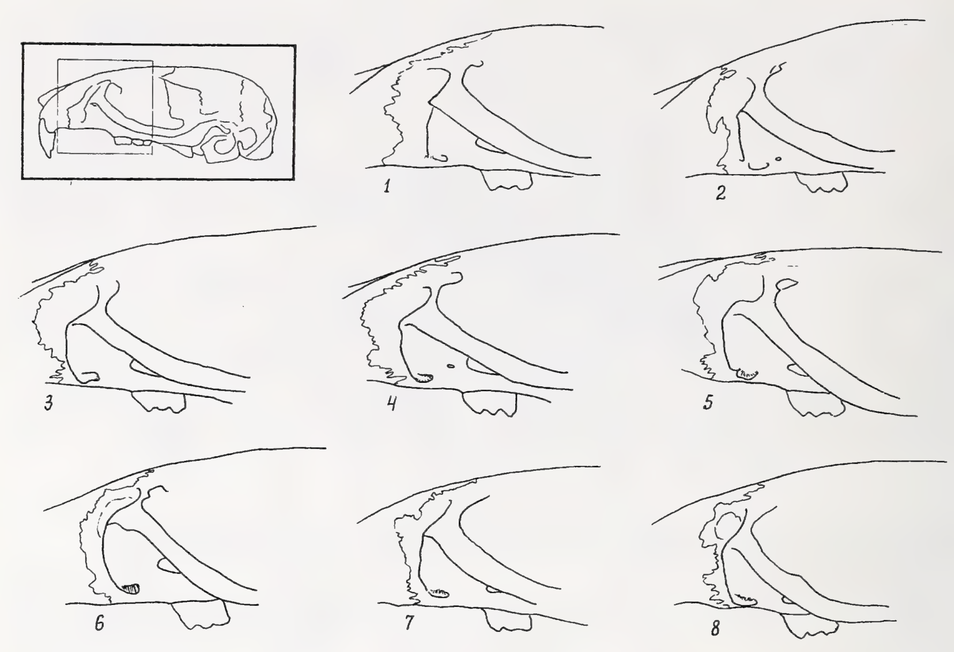


Fig. 7. Shape of masseter plates in house mice from different regions (collection of Zoological Museum of the Institute of Zoology, National Academy of Sciences of the Ukraine). *M. domesticus:* 7: Germany (No 10 031); 8: Germany (No 10 032); 5: Georgia (No 700); *M. praetextus*: 3: Syria (No 10 033); 4: Syria (No 10 030); 6: Azerbaijan (No 437); *M. musculus*: 1: Ukraine. Kiev (No 33); 2: Ukraine, steppe region.

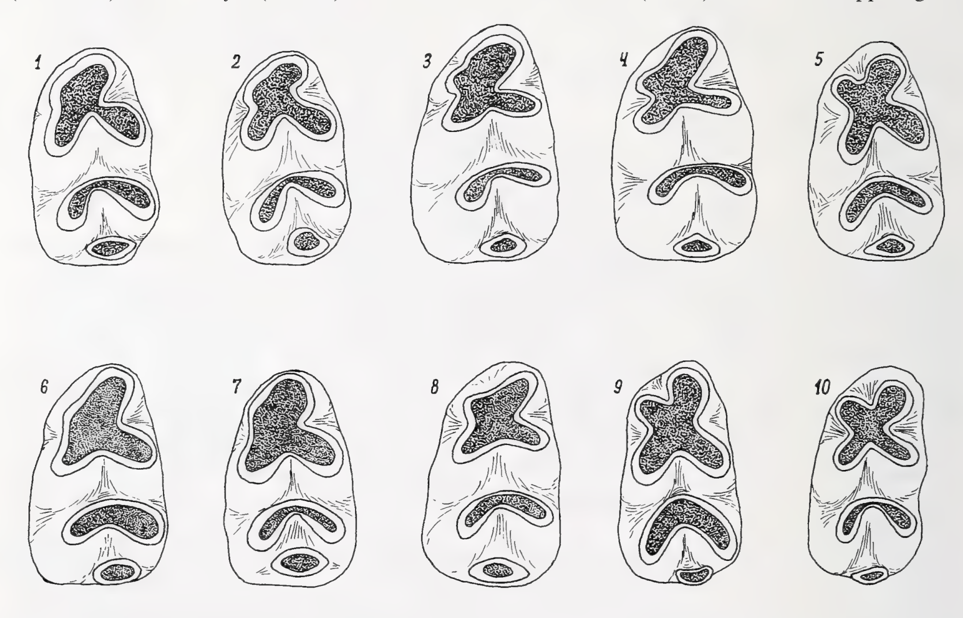


Fig. 8. Variation of M_1 occlusal surface in house mice from different regions (collection of the Zoological Museum of Institute of Zoology, National Academy of Sciences of the Ukraine): *M. domesticus* 1: Germany (No 10 031); 2: Germany (No 10 032); 6: Georgia (No 557); 7: Georgia (No 558); 8: Georgia (No 700); *M. praetextus* 3: Syria (No 10 033); 4: Syria (No 10 030); 5: Azerbaijan (No 436); *M. musculus* 9: Ukraine, Kiev (No 13); 10: Ukraine, steppe region (No 33).

Generalisation of geographic variation data according to climatic zones

In the occidental part of the Transcaucasus with a moist subtropical climate, where genes of *M. domesticus* predominate, house mice are characterised by dark bellies, sometimes with white spots, and by tails equal or longer than heads and bodies together, while in the oriental Transcaucasus, with a climate similar to dry subtropics, populations of white-bellied and rather long-tailed mice occur with a relatively high level of *M. domesticus* genes. Typical *M. musculus* populations dwell in continental steppe regions of the Ciscaucasus. These mice have all morphological and genetic characteristics inherent to this species. The climate of Daghestan is intermediate between the Cis- and Transcaucasus. The gene pool of these populations is practically identical to *M. musculus*, but some specimens have certain morphological features (mainly the tail length and belly colouration) typical for *M. domesticus*.

Discussion

Taxonomy of Caucasus house mice

High frequency of alleles Es-1^{98}, Es-2^{103}, Idh-1^{95}, large body size, relatively long tail, belly colouration, and some cranial features of the house mice dwelling in the Transcaucasus prove their identity to southern house mice species (*M. domesticus* or *M. praetextus*).

The sharp contrast between mice dwelling in the eastern and western parts of the Transcaucasus indicates the existence of two southern house mice species in this region. There are also two forms occurring in the Transcaucasus. Specimens of the occidental form, *M. m. formosovi* Heptner, 1930, are characterised by: large body size; dark belly and back with albino spots, and lacking a distinct borderline of colouration; usually tail longer than head and body, long feet and ears; fairly massive skull with a wide interorbital space; masseter plate in the angular form. In some mice from the most southern localities a characteristic three looped pattern on the occlusal surface of the M_1 was found. All of these features confirm the identity of *M. m. formosovi* to *M. domesticus*. In the Caucasus region it occurs in Georgia, Armenia and penetrates into Daghestan. The second geographic form is traditionally identified in Transcaucasus under different names, such as: *M. m. bactrianus* Blyth, 1846 (Satunin 1905), *M. m. tataricus* Satunin, 1909 (Heptner 1930; Argiropulo 1940; Vereschagin 1957), or *M. m. praetextus* (Shidlovsky 1976). It is a large white-bellied mouse with a tail length, equalling to that of head and body, large hind feet, and moderate ear lengths. The skull is not massive, the interorbital space is of intermediate width, and the masseter plate is round in shape. It mainly occurs in Azerbaijan steppes.

Mice living in Ciscaucasus and, probably in some semidesert and mountainous regions of the Transcaucasus, were identified as *M. m. wagneri* Eversmann, 1848 by Satunin (1905); *M. m. hortulanus* Nordmann, 1840 by Argiropulo (1940), and Vereschagin (1957), and *M. m. musculus* by Shidlovsky (1976). The specimens can be characterised by: a rather small body size; grey or white belly contrasting with the back; short tail (60–90%) and feet; and small ears. The skull has a small size, narrow interorbital width, an angular or slightly rounded masseteric plate. The occlusal surface of M_1 has a four looped pattern.

The *M. musculus–M. domesticus* hybrid zone

As noted above (Milishnikov et al. 1990), the main peculiarity of the Transcaucasian hybrid zone consists in an unusually great extent of introgression of *M. musculus* and *M. domesticus*. While in Europe the hybridisation zone does not exceed several dozens

kilometres (Hunt and Selander 1973; Kraft 1984; Vanlerberghe et al. 1988), in the Transcaucasus it is more than several hundred kilometres. In this case, it is quite probable, that the geographic distribution of *M. musculus* genes is not limited by the border of the former USSR but extends still farther south throughout Asia Minor to the Mediterranean, where they are regularly recorded at low frequencies (Thaler et al. 1981; Britton-Davidian 1990).

The distribution of individuals morphologically identical with *M. domesticus*, and having genes inherent to this species, is limited within the territory of the former USSR to the Transcaucasus, since in the north of the Great Caucasian Ridge genetically and morphologically homogeneous *M. musculus* populations occur. A sharp boundary in the distribution is most likely due to climatic transition from the subtropics of the Transcaucasus to the continental steppe regions of the northern Caucasus. Thus, climatic boundaries in this region determine the subdivision of superspecies *M. musculus* s. l. into the southern forms *M. domesticus* and *M. praetextus* and the northern *M. musculus.* While the northern species is homogeneous genetically and morphologically, the southern forms represent a complicated hybrid complex, including genes of both *M. musculus* and *M. domesticus.* Thus, in this region there is no clear subdivision into *M. musculus* and *M. domesticus* as in the case of Europe. It should be emphasised that this boundary is not only geographical, passing along the Great Caucasus but rather climatic. This is confirmed by penetration of *M. domesticus* genes into southern Daghestan, where the climate is similar to subtropical, and by penetration at the biochemical level of homogeneous *M. musculus* specimens (Frisman et al. 1990) to eastern Azerbaijan on the Apsheron Peninsula, in the region with dry continental climate.

The geographical distribution of different house mice species in the Transcaucasian region supports the importance of climatic borders (Klein et al. 1987) in the determination of house mice areas and attachment of *M. musculus* to continental regions and *M. domesticus* to moist ones, similar to subtropical conditions.

The *M. domesticus–M. praetextus* hybrid zone

The presence of grey-bellied mice in the Central Transcaucasus, sharply contrasting in colouration with occidental dark-bellied and oriental white-bellied forms, indicates hybridisation of *M. praetextus* and *M. domesticus.* In this case the hybrid zone is also not limited by several dozens kilometres, since grey-bellied long-tailed mice occur not only in the Central Transcaucasus (the border of Georgia and Azerbaijan in this case), but also in the south of Azerbaijan (in the Lenkoran). In this region fairly dark-bellied mice live along with white-bellied. This fact is due to penetration of *M. domesticus* along the mountaineous regions of the Small Caucasus or, presumably, their import by man.

Analysis of habitat preferences resulted in the following. As compared with *M. praetextus*, *M. domesticus* (*M. m. formosovi*) is more closely connected in the Transcaucasus with human structures (Shidlovski 1976), which accounts for its penetration throughout the Great Caucasus and Daghestan. *M. praetextus* is an indigenous form, dwelling mostly in steppe landscapes (Shidlovski 1976). It is distributed in Azerbaijan, where there are true steppes. Thus, each of the species is associated with its own habitat: *M. domesticus* is a synantropous form, living in the immediate vicinity of human houses, and *M. praetextus* is a more indigenous steppe form, which presumably penetrated from Iran, where similar specimens inhabit natural landscapes (Schwartz and Schwartz 1943), similar to Azerbaijanian ones. Hence, in contrast to the *M. musculus–M. domesticus* species, the *M. domesticus–M. praetextus* introgression zone is stabilised by landscape-biotopical factors.

Comparative characteristics of European and Asian hybrid zones

On the basis of biochemical genetical studies of both European and Asian hybrid zones, it was possible to analyse the structure and genetic processes in these zones in detail.

The European zone is a result of hybridisation of two species, *M. domesticus* and *M. musculus.* Its width is approximately a few dozen kilometres and does not exceed 50 kilometres (Selander et al. 1969; Kraft 1984; Vanlerberghe et al. 1986, 1988; Nance et al. 1990). There is a tendency toward limitation of hybridisation in the European zone. Thus, a previous study showed that mitochondrial DNA introgression occurs in one direction only, that is from *M. musculus* to *M. domesticus* (Vanlerberghe et al. 1988). Moreover, it has been shown (Vanlerberghe et al. 1986, 1988; Nance et al. 1990) that no chromosome introgression occurs. There has been a direct observation supporting assortive breeding in hybrid *M. musculus* and *M. domesticus* species performed in Bulgaria (Vanlerberghe et al. 1988; Nance et al. 1990). This has been confirmed by heterozygous deficit at diagnostical loci.

Hybridisatian in the Transcaucasus takes place among three parapatric species, *M. musculus*, *M. domesticus*, and *M. praetextus.* The width of this hybrid zone is more than several hundred kilometres. This circumstance transformed it from a hybrid zone into a zone of gene introgression. There is a narrow transitional zone along the Great Caucasus between the homogeneous Ciscaucasus *M. musculus* populations and the Transcaucasus zone of gene introgression. This border between the zone of hybridisation and homogeneous *M. musculus* populations corresponds well to the subdivisions by climatic zones. Thus, specimens of the northern species dwell in drier and more continental re-

Table 3. Comparative characteristics of hybrid house mice zones of Europe and Asia

Characteristics	Hybrid zones		
	Europe	Transcaucasus	Eastern Asia
Hybridising species	*M. musculus* – *M. domesticus*	*M. musculus* – *M. domesticus* – *M. praetextus*	*M. musculus* – *M. castaneus*
Width of hybrid zone	not more than 50 kilometres	more than 300 kilometres	more than 1 000 kilometres in latitude
Expressiveness of border between hybrid zone and parental species	border is well-expressed	only the border between *M. musculus* and introgression zone	sharp transition between parental species and hybrid zone is absent
Intrapopulation mechanisms limiting interbreeding	present	not found	absent
Correspondence geography of hybrid zone to climate borders	*M. musculus* dwells in drier continental regions while *M. domesticus* prefers moister regions with oceanic climate	accumulations of *M. domesticus* genes and morphological features take place in subtropical regions	higher concentrations of *M. castaneus* genes and expressiveness of some morphological features are observed in warmer and moister climate
Possible mechanisms of hybrid zone stability	first of all, there are biological barriers	climate factors, biological barriers are unknown	only climatic factors
General characteristics	typical hybrid introgressive zone between parapatric species	complicated formation which is not presented by classical narrow hybrid zone	gradual transitional zone between two species identified at biochemical gene level

gions while specimens with genes and morphological characteristics of southern forms occur only in subtropical regions. No tendencies toward limitation of gene flow in the Transcaucasus between specimens of the three species were found.

Gene introgressions between the eastern Asian house mouse form *M. castaneus* and the northern Palearctic *M. musculus* have been found in Japan (Bonhomme et al. 1989) and in some parts of the Russian Far East (Frisman et al. 1990), initially in the Vladivostok region (Frisman and Korobitsina 1990). The estimated width of introgression zones was at least three hundred kilometres. These observations were confirmed by morphological investigations also. Thus, in the Russian Far East localities, where alleles of *M. castaneus* predominate, specimens are characterised by a long tail and "*castaneus*"-like belly coloration (Frisman et al. 1990). The geographical distribution of house mice species in eastern Asia (Bonhomme 1986) and data concerning the localisation of the hybrid zone suggest that the zone of gene introgression in a North-South direction between *M. castaneus* and *M. musculus* can be more than one thousand kilometres wide.

Comparison of hybrid zone biological peculiarities confirmes significant differences in structure of European and Asian hybrid zones, especially, in their sizes. So, in Europe the *M. musculus – M. domesticus* hybrid zone width does not exceed some tens kilometres. In the Transcaucasus, where hybridisation takes place between *M. musculus*, *M. domesticus*, and *M. praetextus*, it is more than 300 hundred kilometres. In eastern Asia the interstitial zone between *M. musculus* and *M. castaneus* most probably is more than one thousand kilometres. Therefore, the concept of narrow hybrid "zone" is not appropriate for Asian territories. Actually, these are zones of gradual transitions between the above-mentioned species. It can be characterised by gradual changing of the gene frequencies and intermediate morphological features of specimens according to climate.

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Zusammenfassung

Die Hybridzone der Hausmäuse Mus musculus s.l. in Transkaukasien

Die Hybridzone der Hausmausarten in Transkaukasien wird auf der Grundlage von Allozymdaten und morphologischen Merkmalen beschrieben. Es wird aufgezeigt, daß die Hybridzone in Transkaukasien von drei parapatrischen Arten gebildet wird: *M. musculus*, hauptsächlich im Nordkaukasus beheimatet, *M. domesticus*, die vom westlichen Transkaukasien bis zum östlichen Kaukasusvorland zu finden ist und *M. praetextus*, weit verbreitet in den Steppen Aserbaidshans. Wesentliche Besonderheiten dieser Hybridzone sind: 1) die ungewöhnliche Ausdehnung der Zone der Genintrogressionen; sie umfaßt das gesamte Transkaukasien; 2) die schmale Grenze zwischen *M. musculus* und der Zone der Genintrogressionen zwischen *M. musculus*, *M. domesticus* und *M. praetextus*, die sich entlang der Klimagrenze zwischen der kontinentalen und subtropischen Region erstreckt und 3) das Vorhandensein einer Übergangszone zwischen *M. praetextus* und *M. domesticus* in Zentraltranskaukasien. Die gewonnenen Ergebnisse werden im Vergleich mit den Besonderheiten der Hybridzonen in Europa und Ostasien dargestellt. Der Schwerpunkt liegt dabei auf zwei wesentlichen Besonderheiten der Hybridzonen Europas und Asiens, ihrer nach europäischen Maßstäben ungewöhnlichen Breite und ihrer Lokalisierung in Gebieten mit nahezu subtropischem Klima.

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Population dynamics of the Common opossum, *Didelphis marsupialis* (Mammalia, Marsupialia), in southern Brazil

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Nowadays, the majority of the American marsupial species is found distributed in the Neotropical Region and included in three families (Kirsch 1977). The common opossum, *Didelphis marsupialis* Linnaeus, 1758, one of these marsupials, shows a clear neotropical distribution occurring from Mexico to northern Argentina (Hershkovitz 1969). Despite its abundancy in urban environments (Husson 1978), the main studies concerning the population dynamics of the common opossum in Brazil were carried out by Davis (1945), Cerqueira et al. (1993), and Cherem et al. (1996). Thus, as there is little demographic data available to understand the general ecology of this opossum, this study aims to verify its sexual rate, age structure, population density, recruitment, and mortality.

This study was carried out in an area of Curitiba City, State of Paraná, southern Brazil (25°25′ S and 49°18′ W), at 940 m above sea level. The area has five hectares covered with mixed ombrophyllous forest, and it has many roads, houses, and buildings in the vicinity. The mean annual temperature is 16.5 °C (Maack 1981). It is possible to define two distinct seasons in Curitiba City, the dry season (April to August) and the wet season (September to March), in accordance with climatic data obtained at the Meterorological Station of the Universidade Federal do Paraná, 8 km distant from the study area.

Opossums were captured in 30 live traps (40×20×20 cm) that were uniformly placed in the study area between February 1995 and January 1996. These live traps were baited during the afternoon and observed for opossum captures the following morning once per week. The bait was ripe banana with peanut butter and codfish liver oil. After capture, animals were sexed, aged (Tyndale-Biscoe and Mackenzie 1976), marked by combinations of holes in each ear and released. Sexes of pouch young were determined taking care not to detach them from teats. A binomial distribution test (Zar 1984) was utilized to verify if there was a significant difference between expected (1:1) and observed sexual rates. For a better understanding of the age structure, the opossum permanence in the area was verified taking into account the time between the first and the latter capture day of each individual. The immigration rate was obtained by taking the proportion of the number of new individuals captured during each period of two months divided per the total of individuals in the area during the last two months. Inversely, the emmigration rate was obtained by taking the individuals that were not recaptured during each period of two months. The density and migration rates were based on the minimum number known to be alive in the study area. The mortality was verified through direct observation in the study area and its surroundings during the field phases.

After 12 months of studies, 1761 baited traps resulted in 192 opossum captures. The estimated population size was 18 opossums, with 11 females and seven males (1.6 females: 1.0 male). Utilizing the binomial distribution test (Zar 1984), the sexual rate observed for adults and subadults did not differ significantly from the expected rate ($P > 0.12$). The same occurred for pouch young ($P > 0.10$) with 25 females and 21 males (1.2 females: 1.0 male).

Juveniles and subadults (all less than one year old) were captured during the end of the wet season and the beginning of the dry season, respectively. Some of them (three females) remained in the area until the adult stage (seven to 12 months). Two older adult females were recaptured for a time longer than eight months. Adult males (about one year old) and females with pouch young were captured mainly during the wet season (September to January and August to January, respectively). Males remained in the area for three months at maximum.

The mean population density was 1.4 opossums/ha (range: 0.8 to 2.2 individuals/ha). The immigration rate showed a positive correlation with the density ($r = 0.91$, $P < 0.05$). The emmigration rate did not contribute to density fluctuations ($r = 0.00$, $P < 0.05$). Based on births, the density was high during August and November (8.2 and 6.8 pouch young/ha, respectively), and was zero from February to July.

There were two common opossum deaths in the area. One death was as a result of human contact. On the other hand, several *D. albiventris* Lund, 1841 were found dead on roads near the study area.

Sexual rates observed here corroborate some other studies on *Didelphis* (Stout and Sonenshine 1974; Atramentowicz 1986; Cherem et al. 1996). However, there was an untested trend for a greater number of female opossums in the population (see Holmes and Sanderson 1965; Atramentowicz 1986). The higher rate of females in the study area is most probably related to this trend. Studies of Davis (1945), Atramentowicz (1986), Sunquist et al. (1987) and O'Connell (1989) also revealed greater female permanence in other regions. The absence of males in the study area during the dry season is probably related to non-oestrous females that possibly avoided them during this time (see Motta et al. 1983). The study of Ryser (1992) on *Didelphis virginiana* Kerr, 1792 gives some evidence to support this, with females showing stable home ranges and males increasing theirs during the breeding season while seeking for mates.

The presence of pouch young was only observed during a certain period of the year. This is in agreement with studies of Fleming (1973), Tyndale-Biscoe and Mackenzie (1976), Cerqueira et al. (1993), and Cherem et al. (1996) concerning the same species. Juveniles were also seasonally captured, which is in agreement with the study of Fleming (1972) in Panamá. The common opossum probably showed this population pattern in response to advantages that their young gain if they are weaned during a season with widely available resources (see Fleming 1973; Julian-Laferriere and Atramentowicz 1990). Some cited evidences of seasonality in the population succession were already reported by O'Connell (1989) and Cerqueira et al. (1993) from other sites in South America.

Our observations in southern Brazil were in accordance with other authors that reported a rapid turnover, every two or three years, for the common opossum in northern South America (Atramentowicz 1986; Sunquist et al. 1987; Sunquist and Eisenberg 1993). Hence, we noticed that the great majority of captured opossums originated from the preceeding breeding season as reported by O'Connell (1989) from Venezuela.

Except for the study of August (1984) in the llanos of Venezuela, other estimated densities for the common opossum (Fleming 1972; Charles-Dominique et al. 1981; Atramentowicz 1986; Sunquist et al. 1987; O'Connell 1989; Cerqueira et al. 1993) were similar to the density verified here.

Considering the greater difference between the high densities of pouch young and the

low abundance of independent opossums in our field area, it is probable that relatively few individuals survive until maturity, which is in agreement with data of Atramentowicz (1986).

The main factor of opossum mortality in the study area was human action. Based on our data, the common opossum must be less often run over by cars than the white-eared opossum in Curitiba City. Gardner (1983) reported that the common opossum is often run over by cars in Costa Rica. On the other hand, Atramentowicz (1986) and Sunquist and Eisenberg (1993) reported that the main mortality causes in natural environments outside urban areas are wild predators.

Therefore, the common opossum showed a population dynamic subject to seasonal variations, exhibiting a population density strongly related to births and immigrations. Evidences of sexual demographic differences were observed, with females tending to remain in forested sites, when the species occurs in urban environment. This trend may reflect an attempt to better guarantee reproductive success in these sites.

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Z. Säugetierkunde **63** (1998) 173–178



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Bemerkungen zu den intraspezifischen und interspezifischen Beziehungen Hirngewicht – Körpergewicht sowie Rückenmarksgewicht – Körpergewicht bei Caniden.

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Haller (1762) stellte fest, daß in einem nahen Verwandtschaftskreis die kleinen Arten relativ schwerere Gehirne besitzen als die großen. Seit Ende des 19. Jahrhunderts wird die Beziehung Hirngewicht (HG) – Bruttokörpergewicht (BKG) intensiv diskutiert (Snell 1892; Dubois 1898; Lapique 1898; Klatt 1921). In der Folgezeit wurde eine große Zahl von Arbeiten zu dieser Problematik publiziert (Pirlot 1987). Es stellte sich heraus, daß die Hirngröße abhängig ist von der Körpergröße, aber auch von der Organisationshöhe und möglichen Spezialisationen der Gehirne. Diese quantitativen Zusammenhänge lassen sich mit der Allometrieformel beschreiben:

$$\log HG = \log b + \log a \cdot \log BKG$$

a ist Ausdruck für die Abhängigkeit des HG vom BKG; b zeigt das Ausmaß der Faktoren, welche außerdem das HG bestimmen.

Zur Beurteilung der Organisationshöhen und möglichen Spezialisationen der einzelnen Arten ist zunächst der Einfluß des BKG auf das HG zu bestimmen. Für den interspezifischen Bereich kann dies nur geschehen durch die Berechnung des a-Wertes für unterschiedlich große Arten naher Verwandtschaft, die sich möglichst nur in der Körpergröße unterscheiden. Auf diese Weise konnte für viele systematische Einheiten der Säugetiere ein a von ~0,566 nachgewiesen werden (Röhrs 1985, 1986). Bei Gleichheit der a-Werte ist es möglich, die b-Werte der verschiedenen Arten direkt miteinander zu vergleichen. Der b-Wert einer systematischen Einheit wird = 100 gesetzt, Abweichungen hiervon sind Ausdruck unterschiedlicher Organisationshöhe oder Spezialisation der Gehirne. Worauf diese Abweichungen zurückzuführen sind, muß durch quantitative Analyse der einzelnen Funktionssysteme der Gehirne ermittelt werden. Voraussetzung hierbei ist wiederum die Feststellung der Abhängigkeit der Größe der Funktionssysteme von der Körpergröße.

Zur Überprüfung von Domestikationswirkungen auf die Hirngröße verglichen Klatt (1921) und Klatt und Vorsteher (1923) Hirngewichte von Wölfen und Haushunden. An einem umfangreichen Datenmaterial wurde gefunden, daß bei Haushunden für die Beziehung HG-BKG ein a von ~0.25 gültig ist. Klatt beurteilte diesen überraschend niedrigen Wert als Ausdruck einer Domestikationswirkung. Er war der Meinung, daß ein a von 0.56 bei Wildarten sowohl intraspezifisch als auch interspezifisch gültig sein müsse. Bei funktioneller Betrachtungsweise ist diese Auffassung durchaus verständlich.

Herre (1956) vertrat die Auffassung, daß ein a von 0.25 auch innerhalb von Wildarten gültig sei. Für einen eindeutigen Beweis dieser Annahme fehlte damals aber noch ausreichendes Untersuchungsmaterial. Geeignete Daten von unterschiedlich großen adulten Individuen einer Wildart konnten zunächst für Rotfüchse beschafft werden (Herre/Röhrs, Anatolien 1953; Röhrs, Schweden 1955). Bei 51 Rotfüchsen ergab sich für die Beziehung HG-BKG ein a von 0.22 (Röhrs 1959), für 120 Individuen ein a von 0.252 (Röhrs 1986). Dieser niedrige intraspezifische a-Wert von etwa 0.25 wurde bei ausreichendem und geeignetem Datenmaterial für weitere Wildarten, auch für die Stammarten von Haustieren und deren domestizierte Formen bestätigt. (Ebinger 1972; Ebinger et al. 1984; Röhrs 1986; Röhrs et al. 1989). Damit war eine Basis geschaffen für den intraspezifischen Vergleich der Hirngewichte von Wild- und Haustieren, es konnte das Ausmaß der Hirngewichtsabnahmen bei den einzelnen domestizierten Arten durch die Domestikation bestimmt werden. Das gilt auch für die Änderungen von Teilstrukturen der Gehirne, da sie nach bisherigen Kenntnissen ebenfalls bei Wildarten und ihren Haustieren jeweils gleiche Abhängigkeiten vom BKG zeigen (Ebinger 1974, 1995; Kruska 1980; Herre und Röhrs 1990). Die Übereinstimmung der a-Werte macht es auch möglich, das Ausmaß der Hirngewichtsabnahmen sowie der Teilstrukturen bei den einzelnen Haustieren direkt miteinander zu vergleichen, was bei starken Abweichungen von den typischen intraspezifischen a-Werten nicht möglich wäre. Es ist kaum zu verstehen, weshalb die Beziehung HG-BKG für den intraspezifischen Bereich so stark von der interspezifischen abweicht. Der interspezifische Wert von 0.566 läßt funktionelle Interpretationen zu, z. B. etwa Oberflächenproportionalität zum Körpervolumen. Beim intraspezifischen Wert von

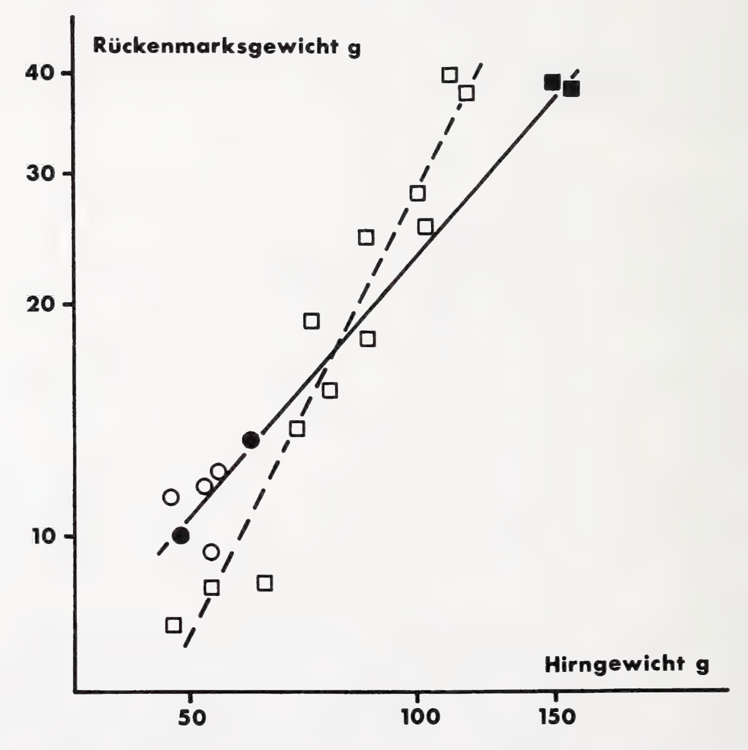


Abb. 1. Intraspezifische Beziehung Rückenmarksgewicht – Hirngewicht bei Haushunden □, - - - a = 2.059. Interspezifische Beziehung Rückenmarksgewicht – Hirngewicht bei Caniden, ○ *Vulpes vulpes*, ● *Canis aureus*, ■ *Canis lupus*, — a = 1.156.

a = 0.25 könnte man zu der Vorstellung einer neuronalen „Überversorgung" der kleinen Individuen einer Art und der neuronalen „Unterversorgung" der großen Individuen kommen. Ein adulter Andenfuchs mit 4 000 g BKG hat ein HG von ~ 53 g, ein adulter Andenfuchs mit 9 500 g BKG hat ein HG von ~ 66 g. Es kann spekuliert werden, ob innerhalb von Arten eine bestimmte genetische Konstellation vorhanden ist, nach der das Unterschreiten eines bestimmten Minimums und ein Überschreiten eines bestimmten Maximums der Hirngröße nicht möglich ist. Dies könnte bedeuten, daß zwischen Gehirnen einer Art eine Körpergrößenabhängigkeit mit annähernd $^2/_3$ Proportionalität besteht und auch eine körpergrößenunabhängige Beziehung, die jedem Gehirn einen konstanten arttypischen Anteil zuweist (Ebinger 1983).

Bei allen quantitativen Analysen des Zentralnervensystems und seiner Funktionseinheiten stand und steht das Gehirn im Mittelpunkt. Zum Zentralnervensystem gehört aber auch das Rückenmark. Daten über Rückenmarksgewichte liegen kaum vor, das hat sicher mit Präparationsschwierigkeiten zu tun. Klatt und Vorsteher (1923) haben Rückenmarksgewichte (RMG) bei Wölfen, Goldschakalen, Rotfüchsen und Haushunden bestimmt. Die interspezifische Beziehung RMG-HG lautet bei Wildcaniden

$$\log RMG = -0.9362 + 1.1559 \cdot \log HG.$$

Die entsprechende intraspezifische Beziehung bei Haushunden lautet:

$$\log RMG = -2.6563 + 2.0592 \cdot \log HG \quad \text{(Abb. 1; Tab. 1).}$$

Der Unterschied im Anstieg der beiden Geraden ist signifikant. Der sehr steile Anstieg (a = 2.06) für die intraspezifische Beziehung RMG-HG bei Haushunden zeigt an, daß die intraspezifischen allometrischen Beziehungen RMG-BKG und HG-BKG nicht übereinstimmen (Abb. 2).

Tabelle 1. Allometrischer Vergleich der Beziehung Rückenmarksgewicht zu Hirngewicht bei Caniden und Haushunden.

I. Test auf Unterschiede in Lage und Anstieg (**Gesamtdaten**)	
N	20
arith. Mittelwert X(log)	1.8752
arith. Mittelwert Y(log)	1.2286
Abweichungsquadrate X	0.5107
Abweichungsquadrate Y	1.1118
Abweichungsprodukt XY	0.7060
Korrelation	0.9369
Anstieg	1.5125
Schnittpunkt	–1.6076
Freiheitsgrade 1	2
Freiheitsgrade 2	16
F für Lage und Anstieg	12.7699
Tab.-Wert für P = 99%	6.2270
	** Unterschied ist signifikant **
II. Test auf Unterschiede im Anstieg	
Anstieg Caniden-Gerade	1.1559
Anstieg Haushund-Gerade	2.0592
Freiheitsgrade 1	1
Freiheitsgrade 2	16
F für Anstieg	24.5988
Tab.-Wert für P = 99%	8.5320
	** Unterschied ist signifikant **

Die Anstiege RMG-BKG für die interspezifische Beziehung bei Wildcaniden und die intraspezifische bei Haushunden unterscheiden sich nicht: a = 0.583 (Abb. 3; Tab. 2).

Da in der Domestikation die a-Werte für die intraspezifische Beziehung HG-BKG und anderer Hirnteile sich nicht geändert haben, dürfte dies auch für das Rückenmark

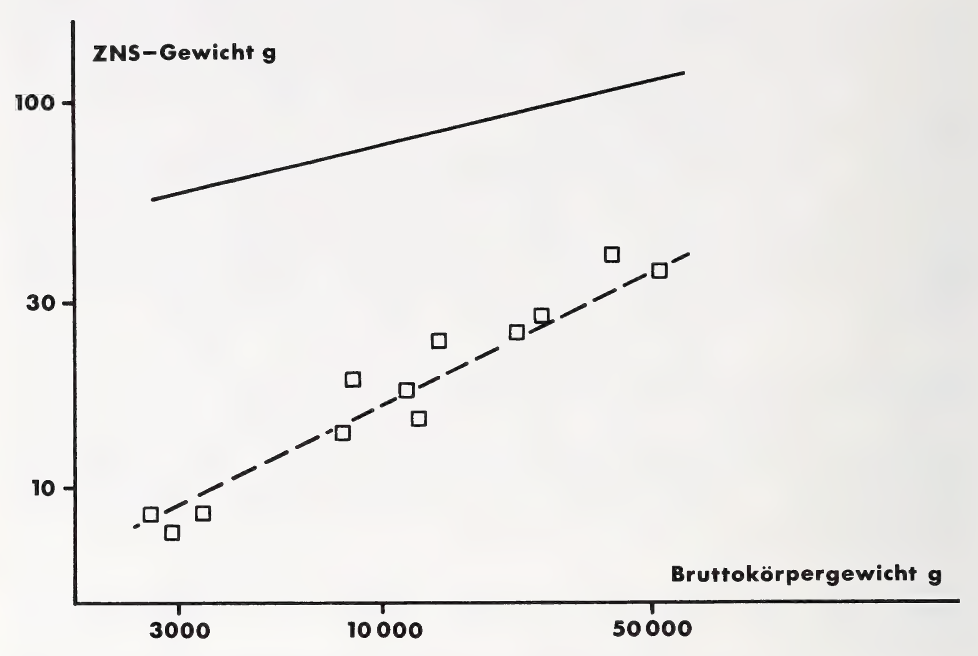


Abb. 2. Intraspezifsche Beziehung Hirngewicht-Bruttokörpergewicht bei Haushunden — a = 0.231 (Ebinger 1980). Intraspezifsche Beziehung Rückenmarksgewicht – Bruttokörpergewicht bei Haushunden - - - a = 0.583.

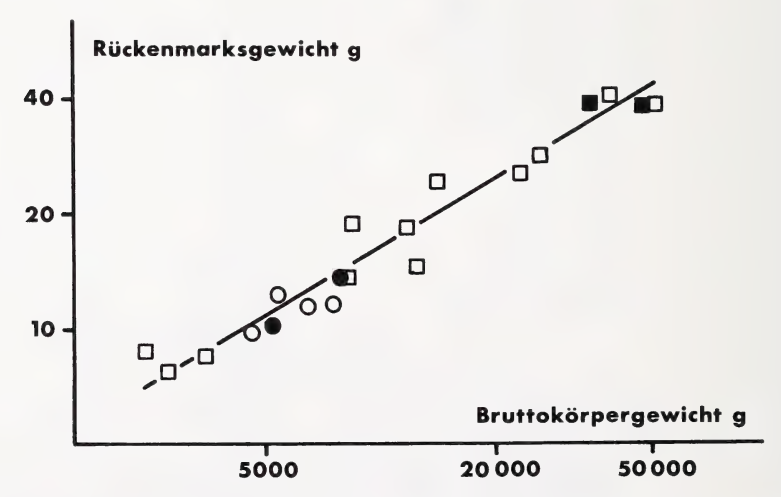


Abb. 3. Zwischen der intraspezifischen (Haushunde) und der interspezifischen (Canidenarten) Allometriegeraden bestehen in der Beziehung Rückenmarksgewicht – Bruttokörpergewicht keine Unterschiede in Anstieg und Lage. Gemeinsames a = 0.583. □ Haushunde, ○ *Vulpes vulpes*, ● *Canis aureus*, ■ *Canis lupus*.

zutreffen; wir gehen davon aus, daß im intraspezifischen Bereich bei Canidenarten für die Abhängigkeit des RMG vom BKG ein a von ~0.58 gültig ist. Dies erklärt zwar nicht die geringen intraspezifischen a-Werte für das HG, zeigt aber, daß auch im intraspezifischen Bereich zumindest für die Organsysteme des Rumpfes eine ausreichende neuronale Versorgung gewährleistet ist. Ein Haushund von 2500 g BKG hat ein HG von ~56,3 g und ein RMG von ~7,1 g; ein Haushund von 50000 g BKG hat ein HG von ~112 g und ein RMG von ~40 g (Abb. 2). Der Anteil des RMG am Zentralnervensystem beträgt bei dem kleinen Hund ~11,2% bei dem großen Hund dagegen ~26,3%.

Für den Vergleich der RMG von Wild- und Haustieren ist ein a von ~0.58 zu verwenden. Beim Vergleich des RMG von Wölfen und Haushunden können somit die interspezifische Gerade der Wildcaniden und die intraspezifische der Haushunde eingesetzt werden. Zwischen beiden besteht auch in der Lage kein Unterschied. Die gemeinsame Allometriegerade lautet:

$$\log RMG = -1.1203 + 0.583 \cdot \log BKG \quad \text{(Abb. 3; Tab. 2).}$$

Demnach hat in der Domestikation bei Haushunden keine Abnahme des Rückenmarksgewichts stattgefunden. Dies bestätigt die Tatsache, daß in der Domestikation progressive Hirnteile weit stärker beeinflußt werden als ursprüngliche. Bei Haushunden beträgt die Abnahme des Hirngewichts 28,8%; die des Prosencephalons 29,9% und die des Tegmentums 13,7%.

Tabelle 2. Allometrischer Vergleich der Beziehung Rückenmarksgewicht zu Bruttokörpergewicht bei Caniden und Haushunden.

I. Test auf Unterschiede in Lage und Anstieg (**Gesamtdaten**)	
N	20
arith. Mittelwert X(log)	4.0292
arith. Mittelwert Y(log)	1.2286
Abweichungsquadrate X	3.1838
Abweichungsquadrate Y	1.1118
Abweichungsprodukt XY	1.8298
Korrelation	0.9725
Anstieg	0.5830
Schnittpunkt	–1.1203
Freiheitsgrade 1	2
Freiheitsgrade 2	16
F für Lage und Anstieg	1.8187
Tab.-Wert für P = 95%	3.6340
	** Kein signifikanter Unterschied **
II. Test auf Unterschiede im Anstieg	
gemeinsame Korrelation	0.9748
gemeinsamer Anstieg	0.5794
Schnittpunkt Caniden-Gerade	–1.1268
Schnittpunkt Haushund-Gerade	–1.0921
Freiheitsgrade 1	1
Freiheitsgrade 2	16
F für Anstieg	1.7725
Tab.-Wert für P = 95%	4.4940
	** Kein signifikanter Unterschied **

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First results on genetic variability in an autochthonous population of Roe deer from a Mediterranean forest in southern Spain

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The Cádiz and Málaga mountains in southern Spain constitute the southwestern limit of the distribution of the roe deer (*Capreolus capreolus* Linnaeus, 1758) (Aragón et al. 1995 a). In this region the species inhabits a Mediterranean xerophytic forest reaching densities from 1.6 to 10.3 individuals per 100 ha (Braza et al. 1994). Anatomical peculiarities have been recorded in this population, both in terms of external morphology (Aragón et al. 1995 b) and craniometry (Aragón et al. 1998), supporting the existence of a Mediterranean ecotype of roe deer distinguished by a dark gray winter fur which turns to reddish or grayish in summer, small size, and short and wide skulls (Braza et al. 1994).

To date, genetic variability in roe deer has been studied mostly in eastern and central European populations (Baccus et al. 1983; Hartl et al. 1991, 1993; Lorenzini et al. 1993, 1996; Wehner et al. 1991). Our aim is to provide the first results on genetic variability for a population living in a Mediterranean forest. There was an absence of introduction of allochthonous individuals in the area or reductions in numbers in recent times. For genetic comparisons, samples coming from north-eastern France (Trois Fontaines, Marne) were used.

A total of 43 blood samples was collected, 25 (18 males and 7 females) from Cádiz and 18 (6 males and 12 females) from Trois Fontaines. After capture of an animal, a blood sample was taken from the jugular vein using a syringe. EDTA was used for preventing coagulation. Aliquots of serum and cells were stored at –20 °C until electrophoresis. Preparation of cell extracts, gel making (starch gel 12%), electrophoretic conditions, and staining procedures followed standard protocols (Pasteur et al. 1987). The following loci were analysed (E.C. numbers are given in parentheses): Ldh-1, -2 (1.1.1.27), Mdh-1 (1.1.1.37), 6Pgd (1.1.1.44), Sod-1, -2 (1.15.1.1), Pk (2.7.1.40), Ak (2.7.4.3), heart-Est, serum-Est (3.1.1.1), Mpi (5.3.1.8), Gpi (5.3.1.9), Hb, and Alb. Results were interpreted following Harris and Hopkinson (1976). Genotype frequencies were obtained directly by scoring the gels.

Four out of 14 loci were polymorphic (Tab. 1). For these loci genotype frequencies were in agreement with the Hardy-Weinberg expectations only at Mdh-1 in Cádiz (Chi-square = 3.81, d. f. = 5, NS). For all other loci there was a deficiency in the number of heterozygotes ($p < 0.001$ for all loci). In Cádiz, no relation was found between the deviation from Hardy-Weinberg and sex or summer appearance of the animals (4 reddish and 12 grayish) (Fisher test for Hb and Pk, and G test for heart-Est). The percentage of poly-

Table 1. Allozyme variability at the polymorphic loci in two roe deer populations from Cádiz (southern Spain) and Trois Fontaines (north-eastern France). Allele frequencies (p), observed single locus heterozygosity (Ho), and expected heterozygosity (He).

Locus	Allele	Cádiz			Trois Fontaines		
		p	Ho	He	p	Ho	He
Mdh 1	A	0.812	0.208	0.312	1.0	0.0	0.0
	B	0.020			0.0		
	C	0.172			0.0		
Pk	A	0.350	0.0	0.455	0.700	0.0	0.420
	B	0.650			0.300		
Heart-Est	A	0.023	0.045	0.429	0.0	0.0	0.0
	B	0.704			1.0		
	C	0.273			0.0		
Hb	A	0.333	0.0	0.444	0.0	0.0	0.0
	B	0.667			1.0		

morphic loci (99% criterium) (P), the observed (Ho) and expected heterozygosity (He) and the mean number of alleles per locus (A) were (± standard errors): P = 28.57%, Ho = 0.018 ± 0.056, He = 0.117 ± 0.195, and A = 1.428 ± 0.755 for Cádiz, and: P = 7.14%, Ho = 0, He = 0.030 ± 0.112 and A = 1.071 ± 0.267 for Trois Fontaines.

Our results confirm that roe deer is one of the most polymorphic species of deer (Lorenzini et al. 1993, six species included). The mean value of polymorphism for Cádiz is one of the highest measured, ranging from 10.5% (Baccus et al. 1983) to 35.7% (Wehner et al. 1991). On the contrary, the degree of heterozygosity in Cádiz is one of the lowest described, ranging from 1.4% (Wehner et al. 1991) to 8.1% (Hartl et al. 1991). The low variability found in Trois Fontaines may be a consequence of human management of the population, living in a fenced area of 1,369 ha.

Habitat use and the social system of the species in areas with a low density of animals may explain the genetic pattern found in Cádiz. In such circumstances adult males exhibit marked territorial behaviour, excluding other males but overlapping with the foraging area of different females. Due to low densities, young males establish territories close to their relatives because free areas are availables (Bideau et al. 1985). This particular spatial pattern may favour inbreeding and, consequently, if the probability of mating with a relative is higher than expected at random, homozygote frequency will increase in the area (Ayala 1975). The genetic variability in the population is maintained by animals which do not find a place close to their relatives, bearing in mind that a single individual migrating among populations per generation is sufficient for preserving homogeneity in allele frequencies (Slatkin 1987).

Table 2. Nei's (1978) genetic identities and standard distances calculated for different populations of roe deer in Europe.

	Identities	Distances	References
Cádiz/T. Fontaines	0.9929	0.0071	Present study
Austria (5 populations)	0.9855–0.9981	0.019–0.0146	Hartl and Reimoser (1988)
Central Europe (20 populations)*	0.9774–1	0–0.0226	Hartl et al. (1991)
Italy (4 populations)	0.9870–0.9990	0.001–0.013	Lorenzini et al. (1993)

* Populations from Switzerland, Austria and Hungary.

Genetic distance and genetic identities, calculated following NEI (1978), are similar to those reported for other European populations (Tab. 2), so we conclude, in agreement with LORENZINI et al. (1993), that genetic patterns of differentiation in roe deer populations are caused by ecological and ethological traits, such as breeding biology and dispersal pattern, rather than being a consequence of the existence of genetically well-separated subspecies. However, the results are very preliminary and may be influenced by the low number of loci and individuals analysed.

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Pattern and rhythm of activity in Alpine chamois (*Rupicapra r. rupicapra*) during winter

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Key words: Alpine chamois, activity pattern, activity rhythm, winter

Changes in activity pattern and rhythm may be indicators for negative impacts on an organism, e. g. diseases or external influences (Aschoff 1981; MacArthur et al. 1982; Green and Baer 1990). For this reason we included activity patterns and rhythms in our ongoing research to determine the impact of leisure activities of man on the behaviour of alpine chamois. No studies have yet been performed on this topic. Whereas much information is available on the daily activity of chamois, we have only few evidence of their activity during the night (Boillot 1980).

If activity during the night is part of the behaviour usually shown by chamois, then animals which leave their preferred feeding grounds during daytime because of leisure activities (Schnidrig-Petrig 1994; Ingold et al. 1993) would have restricted possibilities to compensate for reduced feeding time. This could have negative consequences for the animals in winter, when there is a bottleneck in the availability of food.

The aim of this study was to investigate the activity pattern and rhythm of chamois during winter in a region without human leisure activities.

The present study was carried out in the region Augstmatthorn near Interlaken in the Bernese Alps (Switzerland). The area, about 4 km^2, is part of a game reserve. It covers mostly open pastures at an altitude between 1 400 and 2 100 m above sea level. In winter, the steep, sun-exposed slopes are snow free for most of the time. They are inhabited by up to 150 female chamois at this time of the year.

We recorded the activity of seven females and one male chamois in a total of twenty-nine periods of several days (median: 5 days, minimum: 3 days, maximum: 21 days), over a 24 h period from September 1995 to April 1996 and from January to February 1997. The animals were caught with snares and equipped with a radio tracking collar including motion and orientation sensitive sweeps (TXE, Televilt, Sweden). Signals were recorded with a datalogger (RX 900, Televilt), which was installed in the field in a solar-powered electricity station. Each individual was logged continuously for 1 min., then the logger switched to the next one. This resulted in 7 min. of recording time per hour and animal, when all 8 individuals were logged.

We analysed the data after the method worked out by Bächler (pers. comm.). Data were assigned to the categories "activity" (feeding, moving etc.) and "inactivity" (lying). We conducted a fast fourier transformation of the mean value transformed proportions of activity per hour. The results were depicted in periodograms, which plotted magnitudes vs. period lengths of the frequencies found. The magnitude is defined by the sum of the squared parts of the real and the imaginary part of the amplitude. To demonstrate the

daily distribution of activity, we combined the data for the period of 24 hours. Mean values and standard errors were calculated for every hour.

In figure 1 the mean activity over 24 hours and the rhythm of the chamois "Rita" in the period from 31. 1.–7. 2. 1997 are presented as an example. The mean activity shows three peaks, one in the morning, one in the afternoon/evening and a third around midnight. A minimum of activity is found in the early and in the late night. Furthermore, there is a well developed circadian and an eight-hour rhythm. In all observation periods we found rhythms with a period length of 8 hours and in 28 of 29 cases a circadian rhythm, in some cases also other ultradiane rhythms. In all cases, an activity-peak occurred during the night, almost always around midnight. The amplitude of these peaks was mostly lower than those of the two daily peaks. In all cases there were minima of activity in the early and late night.

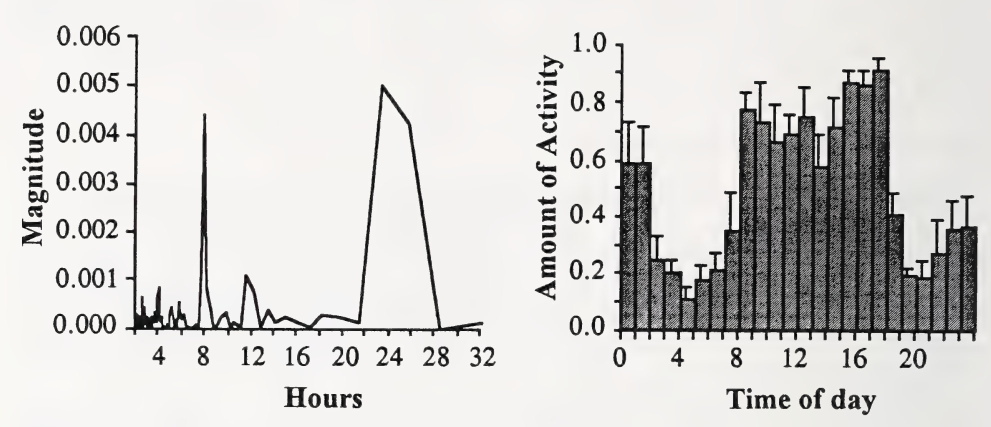


Fig. 1. Rhythm (left-hand side) and pattern of activity of the female chamois "Rita" from 31. 1. to 7. 2. 1997. Rhythms can be recognised as clear peaks. For further explanations, see text.

Although there was some evidence of nocturnal activity of alpine chamois, the regularity of this phenomenon, at least from autumn to spring, is surprising. Simultaneous observations showed that about 75% of activity is feeding. Therefore, we conclude that the results obtained by radio tracking are valid for feeding behaviour also, at least during daylight hours. Whether this proportion of feeding remains at a comparable level during the night remains to be evaluated.

Four of the investigated radio-tracked females were observed on eighteen days during winter 1996/97 from morning to late afternoon. At all times they remained in the open meadows above the treeline. After snowfall they stayed for one or two days at a lower altitude (but still above the treeline) until the snow had disappeared from some places. From morning to late afternoon they only moved over very short distances and remained in a very small area the entire time. The conditions for these animals appear to be ideal: they live in an advantageous winter habitat (open meadows without snow most of the time); they can choose the best places and the best time for feeding since they are not influenced by human activities. Therefore, the activity pattern and rhythm described above seem to represent optimal behaviour for energy balance.

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The karyotype and taxonomic status of *Cryptomys amatus* (Wroughton, 1907) from Zambia (Rodentia, Bathyergidae)

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Key words: *Cryptomys*, Common mole-rats, Bathyergidae, karyotype, taxonomy

Unlike the whole family Bathyergidae, with rather well-understood intrafamiliar systematic relationships but unclear sister-group affinities to other lineages within the Hystricognathi (Honeycutt et al. 1991), the genus *Cryptomys* per se poses no serious problem for taxonomists, yet its intrageneric systematics are difficult and far from being resolved. Thus, for example, the number of species described within the genus was highly author-dependent, ranging from 3 (Nowak and Paradiso 1983) to as many as 44 (Allen 1939) or even 49 (Ellerman 1940). Recently, Honeycutt et al. (1991) have suggested 7 valid species, and their classification has been currently widely accepted (e.g., Woods 1993). Nevertheless, results of karyological and biochemical studies on two yet unnamed *Cryptomys* species from Zambia (Burda et al. 1992; Filippucci et al. 1994, 1997), suggest a need for a revision of the established taxonomic scheme.

Generally, information on karyotypes within the genus *Cryptomys* is scant, the only known data being those on *C. foxi* (Thomas, 1911) (Williams et al. 1983), *C. hottentotus hottentotus* (Roberts, 1913), *C. h. natalensis* (Roberts, 1913), and *C. damarensis* (Ogilby, 1838) (Nevo et al. 1986), *C. darlingi* (Thomas, 1895) (Aguilar 1993), *C. mechowi* (Peters, 1881) (Macholán et al. 1993), and two unnamed species from Itezhi-Tezhi and Lusaka, respectively (Burda et al. 1992). Differentially stained chromosomes were studied to even less extent (Nevo et al. 1986; Aguilar 1993; Macholán et al. 1993).

According to Honeycutt et al. (1991), *Cryptomys amatus*, originally described as *Georychus amatus* by Wroughton (1907), and later ascribed to the genus *Cryptomys* by Allen (1939), is a subspecies of *C. hottentotus* Lesson, 1926. In this study, we present for the first time results of a karyotypic study on small common mole-rats collected at the type locality of *C. [hottentotus] amatus* (Wroughton 1907; Moreau et al. 1945). The diploid chromosomal number and morphology of the chromosomes led us to ascribe these specimens to the distinct species, *C. amatus*, karyotypically separated from other *Cryptomys* species.

In total, 14 individuals (9 males, 5 females) were collected by the road to Chibale, Zambia (S 13°35′; E 30°05′), 1300–1500 m a.s.l. All but a single animal were adult, the only exception being a subadult male. Two males (one "grey" and one "brown", see below) and one female ("grey") were karyotyped. Mitotic metaphases were obtained directly from bone marrow. Slides were differentially stained using the trypsin digestion (G-banding) technique by Seabright (1971), and the C-banding technique by Sumner (1972). Nucleolus organizer regions (NORs) were visualized by the silver-staining method of Howell and Black (1980).

All the animals were captured in cultivated fields, savannah-woodland, and/or savannah-bushland. The collecting site represents a mesic habitat with mid-July temperatures ranging from 10.0 to 12.5 °C and a mean annual rainfall of 944 mm (according to records of the Serenje Climatic Station). The giant mole-rat (*C. mechowi*) occurs sympatrically in this area.

Two colour variants were found at the same site: 8 individuals (5 males, 3 females) were dark grey, whereas 6 individuals (4 males, 2 females) were tan or brown. As no sexual dimorphism in body weight was found within both colour groups, sexes were pooled in the subsequent analyses. The brown animals were heavier ($w = 73.2$ g; $SD = 10.01$; range 52–71 g) than the grey ones (63.3 g; $SD = 8.12$; 61–88 g; the subadult male excluded), but the difference was insignificant (ANOVA: $F = 3.871$, $p = 0.075$). Most animals, irrespective of their overall coloration, had a small or even missing white forehead patch and only few individuals revealed a large patch; in some animals, a white spot was also found on the mentum or belly. Several animals had a rusty-red or brown mentum similar to *C. mechowi*. The infraorbital foramen was elliptical to triangular.

The diploid chromosomal number of all the specimens examined (both "grey" and "brown") was $2n = 50$. Twenty-two pairs of autosomes were biarmed, mostly meta- or submetacentric, except for the first pair which was subtelocentric. Pairs Nos. 17 and 24 were acrocentric but in one of the males, the former appeared to be heteromorphic, one of the elements being subtelocentric rather than acrocentric. The X chromosome was large metacentric, whereas the Y was small and acrocentric ($NF = 96$; $NFa = 92$).

The G-banding and C-banding patterns are shown in figure 1. The Y chromosome revealed a rather inconspicuous G-banding pattern while being wholly positively stained in C-banded metaphases. The X possessed only a tiny centromeric block of heterochromatin. Conversely, most autosomes displayed, in addition to the centromeric heterochromatin, apparent telomeric C-bands (Fig. 1).



Fig. 1. G-banding (left) and C-banding (right) pattern of the karyotype of a male MM 900 ("brown" variant).

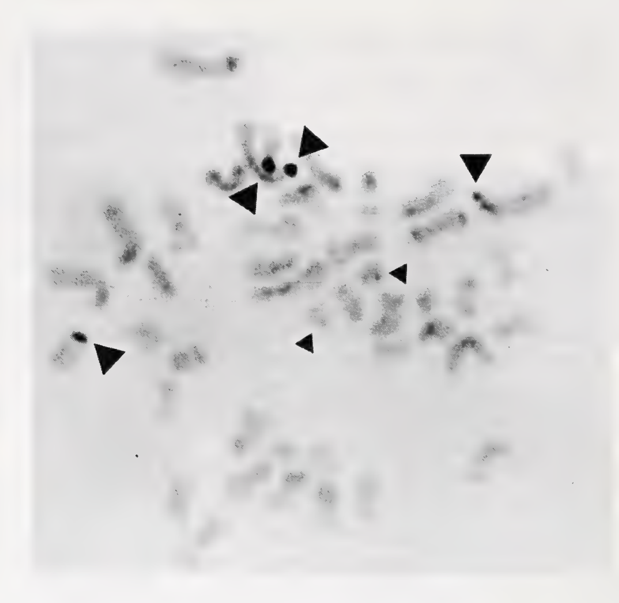


Fig. 2. AgNOR-stained karyotype of a female MM 903 ("grey" variant). Large arrowheads show apparent NORs which were proven to be active virtually in all examined metaphase spreads; in the pair of small autosomes (small arrowheads), the organizers were usually weakly stained or inactive.

Three pairs of autosomes appeared to possess NORs. However, in the smallest NOR-bearing pair (No. 24), the organizers were usually very pale and frequently not active at all. The NORs were located telomerically on the smallest (acrocentric) autosomes and on the short arms of pair No. 1 as well as on a medium-sized submetacentric pair (Fig. 2).

In comparison with two other Zambian species of common mole-rats (BURDA et al. 1992), the specimens examined in the present study were generally smaller, having thicker and more velvety pelages, exhibiting age-independent colour polymorphism, and a great variation in size and shape of the white head spot. However, both the inter- and intraspecific differences were quantitative rather than categorical. Given considerable polymorphisms in the traits traditionally considered diagnostic within the genus *Cryptomys*, it is hard to provide any sound diagnostic keys based solely on the morphological characteristics studied.

The karyotype of *C. amatus* represents one of the lowest known number of chromosomes within the Bathyergidae, the diploid number of *C. mechowi* with 2 n = 40 (MACHOLÁN et al. 1993) being the only exception. Other species of the genus hitherto studied karyologically have shown higher diploid numbers: the "Itezhi-Tezhi" and the "Lusaka" species from Zambia with 2 n = 58 and 2 n = 68, respectively (BURDA et al. 1992), *C. foxi* from Cameroon 2 n = 66 and 2 n = 70 (WILLIAMS et al. 1983), and *C. damarensis* from Namibia and Botswana 2 n = 74 and 2 n = 78, respectively (NEVO et al. 1986). Among the taxa with chromosome numbers closest to that of *C. amatus* are *C. darlingi* from Zimbabwe (AGUILAR 1993), and *C. h. hottentotus* and *C. h. natalensis* from South Africa (NEVO et al. 1986), with 2 n = 54. Irrespective of the same diploid number, however, the morphologies of chromosomes in *C. darlingi* and *C. hottentotus* are very different.

The distinct diploid number and morphology of the chromosomes (see MACHOLÁN et al. 1993 for a review) suggest *C. amatus* can be considered a separate species, karyotypically fairly well differentiated from other species of the genus. Basic characteristics of all the known karyotypes among common mole-rats indicate that these species are geneti-

cally diversified and evolutionarily clearly separated. This seems to be corroborated also by results of allozyme and molecular studies (Honeycutt et al. 1987; Nevo et al. 1987; Filippucci et al. 1994, 1997). However, it is not possible to draw any conclusion as to the closest relatives of *C. amatus* and the evolutionary interrelationships within the genus as a whole solely on the chromosomal data owing to the scarcity of available high-resolution G-banded karyotypes.

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Buchbesprechungen

Schober, W. (1996): **Ultraschall und Echolot. Die Fledertiere der Welt.** 2., veränderte Aufl. Leipzig, Jena, Berlin: Urania-Verlag. 211 S., 123 Fotos (teilweise farbig), 60 Zeichnungen. DM 68,–. ISBN 3-332-00561-8.

In dem vorliegenden Buch ist ein schönes, sehr instruktives und sorgfältig recherchiertes Werk wieder verfügbar, welches in seiner ersten Auflage 1983 von der Edition Leipzig herausgebracht wurde. Wilfried Schober, Leipzig, hat in seinem Werk ein viel weiteres Feld bearbeitet als es der Titel erwarten läßt: Es handelt sich um ein Buch, durch welches der Leser einen umfassenden und detailreichen Einblick in die Biologie der Fledertiere erhält.

Zunächst behandelt der Autor die Beziehung zwischen Menschen und Chiroptera in historischer Vergangenheit und beschäftigt sich mit Fragen wie: „Vogel oder Säugetier?“, „Gottheit oder Dämon?“, ferner geht er darauf ein, daß die Ordnung Chiroptera nicht nur die Microchiroptera (FlederMÄUSE), sondern auch die Megachiroptera (FlederHUNDE) umfaßt. Der bemerkenswerten Vorderextremität der Fledertiere als Flugorgan wird ein eigenes Kapitel gewidmet; ebenso der Verbreitung der Chiroptera. Es folgen Abschnitte, in denen die Megachiropteren und die Familien der Microchiroptera abgehandelt werden. In den folgenden Kapiteln werden dann einzelne Problembereiche aus der Biologie der Chiroptera besprochen: Die biologische und ökologische Bedeutung der verschiedenen Aufenthaltsorte und die Ernährungsbiologie der Fledertiere werden behandelt; gesonderte Erwähnung finden die Beziehungen zwischen Fledermäusen und Fledermausblumen sowie die Erörterung von Dichtung und Wahrheit im Zusammenhang mit den Echten Vampirfledermäusen (Desmodontinae). Die im Titel des Buches angesprochene Problematik von „Ultraschall und Echolot“ erfährt in einem gesonderten Abschnitt, der sich mit den akustischen Fähigkeiten der Fledertiere befaßt, angemessene Darstellung. Ein interessantes Kapitel schildert den Wissensstand über die Fortpflanzungsbiologie und Jungtierentwicklung und ein weiteres beschäftigt sich mit Ortswechseln zwischen Ruhe- und Nahrungs-Orten und Fledermauswanderungen. In einem wichtigen abschließenden Kapitel wird die Notwendigkeit des Fledermausschutzes und die Faktoren, welche die Bestände der verschiedenen Arten gefährden, besprochen („Fledertiere brauchen Freunde“).

Der Informationswert des flüssig und klar geschriebenen, dabei aber nie trivial formulierten, Textes wird durch klare und schön gestaltete Zeichnungen ergänzt. Einen ganz besonderen Genuß bereiten dem Leser die qualitätvollen und oft großformatigen Photographien vieler Chiropterenarten. Es wurden informative und eindrucksvolle „Portraits“ ausgewählt und sorgfältig, in einzelnen Fällen auch sehr ausführlich, beschriftet.

Eine Tabelle zur Systematik der Chiroptera bis zum Familien-Niveau nebst Angaben zur Zahl der heute lebenden Arten, eine Zusammenstellung der Verbreitungsgebiete und der bevorzugten Nahrung der Fledertier-Familien, sowie ein Namen- und Sachwortverzeichnis, eine Seite mit Literaturhinweisen und eine Auflistung der Bildquellen schließen das Buch ab.

P. Langer, Gießen

Carwardine, M.: **Wale und Delphine.** Bielefeld: Edition Naglschmid im Verlag Delius Klasing, 1996. 256 S., 878 farbige Abb., 82 farbige Karten, flexibel geb. DM 58,–/öS 423,–/sFr 52,50. ISBN 3-7688-0949-8.

Das sehr übersichtlich gestaltete Werk ist die deutsche Übersetzung eines im Verlag Dorling Kindersley, London, erschienenen englischen Bestimmungsbuches. Nach einem Vorwort, Angaben zur Handhabung des Buches, einer Kurzbeschreibung der Cetacea, kurzen Angaben zur Anatomie der Wale und zu ihrem Verhalten, sowie nach Bemerkungen zur Erforschung der Cetaceen, zum Artenschutz, zu Problemen der Walstrandungen und zu Beobachtungsmöglichkeiten der Arten, wird in farbigen Übersichtsdarstellungen auf Identifikationsmerkmale der Spezies hingewiesen. Anschließend werden 79 Arten beschrieben. Jeder einzelnen Spezies sind zwei, mitunter auch vier Seiten gewidmet. Nach Nennung des deutschen Artnamens werden in einem knappen Text allgemeine biologische Daten gebo-

ten und anschließend weitere Namen – meist englische – für die behandelte Art genannt. Ein kurzer Abschnitt widmet sich Verhaltensbesonderheiten und ein Absatz beantwortet die Frage, wo mit Aussicht auf Erfolg nach der Art Ausschau gehalten werden kann. Informationen und Abbildungen zur Kopfform, zum Gebiß oder zu den Barten sind ebenfalls zu finden.

Jede Cetaceenart ist mehrfach abgebildet. Eine farbige Darstellung des gesamten Körpers erstreckt sich jeweils über zwei Seiten. Ebenfalls farbige Detaildarstellungen stellen für die Bestimmung wichtige Merkmale heraus; auf Artbesonderheiten wird durch klare Beschriftung besonders hingewiesen. Ferner wird eine Verbreitungskarte geboten. Die beim Schwimmen unter der Wasseroberfläche, sowie beim Abtauchen sichtbaren Körperteile werden gesondert abgebildet und beschrieben.

Zur schnellen Identifikation bei der Beobachtung findet der Benutzer eine farbig herausgehobene „Identifikations-Checkliste". Die Orientierung wird erleichtert durch eine Kopfleiste, in welcher der Name der Cetaceen-Familie und der wissenschaftliche Gattungs- und Artname genannt werden. Ferner werden durch Symbole der Lebensraum, der Häufgkeits-Status, die z. Z. bekannten Populationszahlen und der Grad der Bedrohung dargestellt. Jeweils in der rechten oberen Ecke der eine Art behandelnden Doppelseite sind Angaben zur Körperlänge des neugeborenen und des erwachsenen Tieres zu finden. Eine Fußleiste bietet übersichtlich Angaben zur Größe der Gruppen, in denen die Art aufzutreten pflegt, zur Lage der Rückenfinne, zum Geburtsgewicht und zum Gewicht des erwachsenen Tieres sowie zur Nahrung.

Insgesamt ist das vorliegende Bestimmungsbuch ausgesprochen benutzerfreundlich gestaltet. Ein Glossar und ein Index mit den wissenschaftlichen und den deutschen Namen runden das Werk ab. Bei einer weiteren Auflage, welche dem Werk von Carwadine zu wünschen ist, sollten allerdings störende Druckfehler eliminiert werden!

P. Langer, Gießen

Arlettaz, R.: **Ecology of the sibling mouse-eared bats (*Myotis myotis* and *Myotis blythii*): zoogeography, niche, competition, and foraging.** Martigny, Switzerland: Horus Publ. 1995. 208 pp., 53 Figs., 16 Tabs., 42,– DM. ISBN 2-940141-00-2

Das Große und das Kleine Mausohr ist in weiten Teilen der Palaearktischen Region sympatrisch verbreitet. Beide Arten leben oftmals in enger Beziehung zueinander in den gleichen Wochenstuben und pflanzen sich hier auch fort. Trotz dieser engen Assoziation und trotz ähnlicher Karyotypen gibt es bislang keine Hinweise auf Kreuzungen. Unter 400 biochemisch untersuchten Individuen konnten keine Hybriden gefunden werden. Zwei Probleme stehen am Anfang der Untersuchung: Ist es möglich die beiden Arten nach äußeren Merkmalen sicher zu unterscheiden und läßt sich damit dann die Identität der verschiedenen geographischen Populationen festlegen? (Abschnitte: Identifikation und Zoogeographie). Die vier folgenden Kapitel sind der Ökologie und dem Verhalten beider Arten gewidmet. Wesentlich für die Beurteilung der komplizierten Verhältnisse sind die Untersuchungen über die trophische Nischendifferenzierung der beiden koexistierenden Arten. In dem Abschnitt „Habitat" werden die Ernährungsräume beider Arten in der SW-Schweiz (mit Präferenzen in der Habitatwahl) dargestellt. Im 5. und 6. Abschnitt wird die Frage nach einer möglichen Beuteselektion und der Art des Beutefanges gestellt. Die Besprechung der Ergebnisse im Lichte einer artspezifischen Spezialisierung auf Mikrohabitate und ein ausführliches Literaturverzeichnis verleihen der Arbeit einen monographischen Charakter.

E. Kulzer, Tübingen

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Distribution patterns of the Stone marten (*Martes foina* Erxleben, 1777) in Mediterranean mountains of central Spain

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Abstract

The distribution pattern of the stone marten (*Martes foina*) in a mountainous region of central Spain has been studied. The presence of the species was determined by searching for faeces along footpaths. Variables used in this study were selected in accordance with ecological requirements of the species and landscape descriptions from previous studies.

The distribution pattern was described by Principal Component Analysis (PCA), logistic, and multiple regression techniques. The results indicate that the stone marten is a mainly forest-dwelling species with preference for higher mountainous regions where human density is low. These data agree with previous studies carried out in the Iberian Peninsula and support the hypothesis of niche expansion in Mediterranean areas. They do not corroborate other authors' results, which suggest a preference of this species for urban habitats.

Key words: *Martes foina*, distribution, forest preference, Mediterranean areas

Introduction

Most studies on the ecology of the stone marten (*Martes foina*), especially those relating to diet and space use, have been conducted in central Europe (Libois and Waechter 1991 for a review, see also Clevenger 1994). Little is known, however, about the ecology and distribution patterns of this species in the Mediterranean region at the south of its distribution range (Libois and Waechter 1991). The studies in this area have focused on diet (Delibes 1978; Amores 1980; Ruiz-Olmo and Palazón 1993), and basic aspects of the spatio-temporal ecology of this species (Delibes 1983; Ruiz-Olmo et al. 1991; López-Martín et al. 1992; Genovesi et al. 1996).

In central European regions, the stone marten has been recorded as a species with synanthropic habits which prefers urban areas and villages to all other available habitats (Broekhuizen 1983; Kalpers 1984; Skirnisson 1986; Broekhuizen et al. 1989; Herrmann 1994). In Mediterranean areas, preliminary reports pointed out that this species is less dependent on villages and shifts its preference towards rocky or forest areas (Delibes 1983; Genovesi et al. 1996). These Mediterranean populations could give us important information on the behaviour and ecological characteristics of this species in areas distant from the region of sympatry with the pine marten (*Martes martes*).

The aim of this study was to describe the distribution of the stone marten in a Mediterranean mountain area in relation to forest types, human settlements, and other macrohabitat variables associated with stone marten preferences elsewhere.

Material and methods

Study area

The study area was located in forested habitats of the Guadarrama mountain range (Central Spain), covering a total area of 180,000 ha. This natural area is characterized by steep altitudinal gradients and by a varied human density. As a consequence of the pronounced relief, all the forest types characteristic of central Spain can be found within the area. The lowest level is covered by holm oak (*Quercus ilex*) forest and its serial succession scrub communities (*Cistus*, *Retama*, etc.). This ranges from 600 to 900 m and is the driest area with a dense human population. Between 900 and 1 200 m the Pyrenean oak (*Quercus pyrenaica*) forests are found, which are used as feeding pastures for cattle (dehesas). These forests are dominated by Pyrenean oaks and ashes (*Fraxinus angustifolia*). At the upper level there is a strip in which the oak forests have been replaced by pine trees (*Pinus sylvestris* and other pine species). Pine forests are found up to 1 700 m and have differing degrees of scrub coverage depending on the predominant type of land use. The climate at this altitude is colder and wetter and snow is common. A more detailed bioclimatic and botanic description can be found in Rivas-Martínez (1982).

Survey procedures

The field work was carried out in the winter season (November–March) between 1991 and 1994. The study was conducted over 18 plots (5×5 km each one) that corresponded with areas of homogeneous forest types and physiognomy: 5 plots corresponded to pine forest, 4 to Pyrenean oak forests, and 9 to holm oak forests. The number of plots corresponding to each forest type was proportional to the environmental availability of these forests in the area.

In each plot, sampling was carried out in four different subplots (0.62×0.62 km) in order to obtain an abundance index for each plot (measured as number of subplots with stone marten presence/number of subplots sampled). This type of index can be considered as a frequency of occurence (e. g. Gaston 1991), an appropiate measure of large-scale distribution studies in which just the species presence is of interest. Thus, this abundance index was used for subsequent analyses. In order to cover a wider area and maximize the likelihood of finding the species, two or three different transects (500–600 m long) were defined per subplot area (200 m evenly apart). Along these transects, stone marten faeces were searched for along foot paths and trails which are commonly used by this species (Waechter 1975).

It was considered that the species was present in a plot when at least one subplot had positive results. One subplot is considered as being used when the species was present in at least one of the transects.

Each subplot was visited once each winter and all transects were covered. No changes were detected in the frequency of occurrence of each plot between years (same number of subplots with the species' presence), therefore given values can be considered representative for the distribution pattern of the species in the area.

Variables measures

Each plot (5×5 km) was defined on land-use maps of the Spanish Ministry of Agriculture (1:50,000) and from a series of variables relating to stone marten preferences were measured for each: forest cover (percentage of the whole plot covered by forest); scrub cover (the same for many different types of scrub: *Cistus*, *Cytisus*, *Retama*); pasture cover; mean altitude (altitude calculated as the mean of ten random spots in the plot); roughness index (mean number of 50 m altitude curves counted from a three random west-east line-transects across the plot); human settlement cover (coverage of villages in the entire plot). The cover variables were measured using a 0.5×0.5 km grid superimposed on the land-use map and by counting the number of grids containing each variable type (forest, scrub, human settlement or pasture). The predominant forest type of the plot was also recorded (holm oak, pine or Pyrenean oak forest). The cover variables and roughness index were related to macrohabitat variables associated with preferences of the stone marten in central Europe and Mediterranean areas (e.g. Delibes 1983; Libois and Waechter 1991; Lachat 1993; Herrmann 1994).

Data analyses

We used a Principal Component Analysis (PCA) to describe the distribution pattern of the stone marten in the environmental gradient of these mountains. Also, a stepwise logistic regression (forward Wald Method, NORUSIS 1989) was performed to analyse the associations between PCA factors and presence/absence data in the 5×5 km plots (NORUSIS 1989). In addition, a more detailed stepwise multiple regression analysis (forward) was performed with the frequency of occurrence of stone martens as a response variable and the environmental variables as predictors (NETER et al. 1985). Forest types were categorized as 'dummy' variables (NETER et al. 1985) in this analysis.

All data were normalized prior to the analyses by square root (frequency of occurrence), decimal logarithm (altitude and roughness) and arcsin (cover of forest types) transformations (ZAR 1984). Statistical analyses were performed with the SPSS package for Windows (6.0).

Results

Two factors were obtained from a Varimax rotated PCA with all transformed variables which explained 72.4% of the variance. The first was a gradient from high altitude, high forest and scrub cover, and high roughness index (positive scores), towards areas with a high human settlements cover (negative scores). The second factor segregates scrub (positive scores) and pasture areas (Tab. 1). The stone marten shows a clear distribution pattern where most of the positive plots correspond to positive scores of the first factor (areas of high altitude with low human settlements cover). However, the pattern is clearer when the frequency of occurrence is used. In this case the higher abundances (values of 0.5 or 1) were associated with positive scores of the first factor with only one "outlier" (Fig. 1).

Table 1. Results of the PCA performed with the variables used to study the distribution patterns of the stone marten.

Variable	Factor 1	Factor 2
Altitude	0.855	0.272
Forest	0.603	–0.415
Shrub	0.682	0.940
Pasture	–0.141	–0.772
Roughness	0.762	0.479
Human	–0.809	0.182
Eigenvalue	2.35	1.99
% Explained variance	39.24	33.14

Stepwise logistic regression with the two factors obtained from the PCA showed that only the first factor was significant ($G^2 = 7.4$, 1 df, $p < 0.01$) with 66.7% of the data correctly classified. Stone martens were primarily present in areas with high forest cover and altitude and low human density.

A simple regression between abundance and each individual variable was performed. Only altitude, human settlements cover, and roughness index were significant (Tab. 2). However, the three variables were highly intercorrelated, therefore, only the relationship with altitude was considered (see the correlation coeffcient in Tab. 2). Altitude is also highly correlated with forest type. However, the model obtained from a forward stepwise multiple regression with the forest types (as dummy variables) is more powerful than that obtained from altitude ($R^2 = 83.61\%$ vs $R^2 = 63.61\%$ of the explained variance for forest type and altitude, respectively). Stone martens were more abundant in high areas where the most important forest type is the pine forest (positive coefficient in the multiple regres-

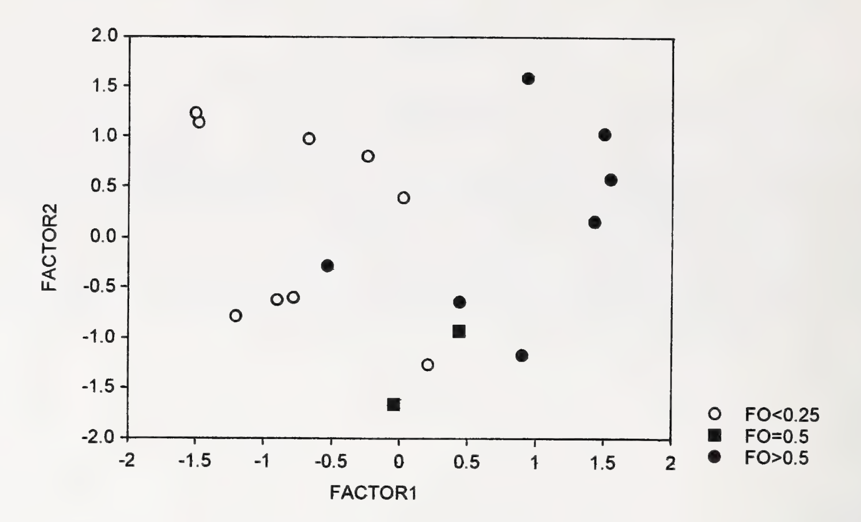


Fig. 1. Plot distribution on the environmental gradient generate from the PCA.

Table 2. Simple Pearson correlations (r) between the frequency of occurrence of the stone marten (FO) in each plot and the used variables.

Variable	Altitude	Forest	Shrub	Pasture	Rough	Human
FO	r = 0.81 p < 0.001	r = 0.34 p = 0.16	r = 0.01 p = 0.96	r = 0.01 p = 0.99	r = 0.66 p = 0.003	r = –0.51 p = 0.03

sion) than lower areas, mostly vegetated by holm-oak forest (negative coefficient in the multiple regression). Most probably, the strong relationship with forest type indicates the association of this species to pine forests, while this association is weak with Pyrenean oak forests (also at higher altitudes than holm-oak forests). Therefore, PCA and regression gave the same relationship between frequency of occurrence of this species and altitude (and their correlated variables: forest types, roughness, and density of human settlements).

Discussion

Our results support the suggestion that the stone marten is principally a forest dwelling species in the Mediterranean region, preferring to inhabit high areas where human settlements are scarce. This implies that, in spite of the fact that this species is not especially adapted to cold weather like the pine marten (Delibes 1983; Libois and Waechter 1991), the stone marten still prefers to inhabit cool areas between 1,200 and 1,400 m. Among the forested areas they showed a clear preference for pine forests (in the highest mountain areas), being rarer in Pyrenean oak and holm oak forests. Their reduced numbers in the lower holm oak woods could be explained by the increased hunting pressure in these areas (especially poisoning and other non-selective control techniques) although its scarcity in some areas with little hunting activity precludes any general explanation for this pattern. The lower abundance in Pyrenean oak forest could be due to habitat structures not studied here (e.g. the lower scrub cover of these habitats compared to others).

The coniferous forests mainly used by the stone marten in our area could correspond physically and structurally to the conifer forests over a large part of Europe (Ozenda

1982). Thus, according to our study its lower frequency of occurrence in these forests elsewhere does not seem to be attributable to the unsuitability of this habitat for this species. Our data do not, therefore, agree with the results obtained by SKIRNISSON (1986) and HERRMANN (1994) which supposed suitability of the urban habitat for the stone marten. On the contrary, only one scat was found near human settlements and the species showed a clear preference for places far away from the more densely populated villages. This appears to be in accordance with the preliminary data of other Spanish researchers (DELIBES 1983; RUIZ-OLMO et al. 1991). Therefore, the suggested advantages in the urban habitat (increased number of refuges and a wider range of available food) may vary in different areas. On the other hand, the effects of other variables that could potentially affect habitat preference, such as intraspecific and interspecific competition and predation risk (MANGEL and CLARK 1986; ROSENSZWEIG 1991), both of which are probably important in the urban areas studied here (dogs and cats are very common), could be evaluated. These variable responses to habitat type have already been shown in the classical works of HEPTNER and NAUMOV (1974) who described the habitat differences between stone martens of the plains (synanthropic) and those of the mountains (forest or rock dwelling).

Could the habitat distribution of the stone marten in Mediterranean areas be explained by a niche shift of this species in a region of allopatry with the pine marten (DELIBES 1983)? This explanation is possible although more detailed studies are necessary to test this hypothesis. However, there are other alternative possible explanation for this shift in preferences. The spatial configuration of habitats and their spatial and temporal availability could influence the distribution patterns and interactions among species (DANIELSON 1991; HANSKI 1995 and references therein). In many of the areas studied in Europe there is a strong historical and present-day human disturbance and there is very low availability of forest habitats on a regional scale. Probably, in this scenario the stone marten would adapt to an environment that is increasingly less forested and could be selectively adventageous to shift its habitat preferences towards urban or rural environments (see HOLT and GAINES 1992 for a theoretical approach). In contrast, in the Mediterranean mountains, forests are historically and currently more abundant and stone martens may select the available habitats according to their suitability. In this scenario, it is probable that the forests can be considered as the most suitable habitat for the stone marten. This hypothesis does not require the existence of competition between the two *Martes* species and future research is needed to investigate the underlying mechanisms that explain the observed pattern.

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Zusammenfassung

Verbreitungsmuster des Steinmarders (Martes foina Erxleben, 1777) in einer mediterranen Bergregion von Zentralspanien

Das Verbreitungsmuster des Steinmarders (*Martes foina*) wird in einer Bergregion Zentralspaniens untersucht. Die An- und Abwesenheit der Art wurde mit Hilfe von Kotfunden auf Fährten durch das Untersuchungsgebiet (5×5 km Plots) bestimmt. Die in dieser Studie benutzten Variablen wurden in

Übereinstimmung mit den ökologischen Ansprüchen der Art und den Faktoren des Makrohabitats der Landschaft ausgewählt.

Die Verteilungsmuster wurden mit Hilfe von PC-Analysen sowie logistischen und multiplen Regressionen beschrieben. Die Analysen zeigten, daß der Steinmarder eine hauptsächlich waldbewohnende Art ist, mit einer Vorliebe für höhere Bergregionen mit geringer menschlicher Besiedlung. Die Ergebnisse stimmen mit früheren Arbeiten überein, die auf der Iberischen Halbinsel durchgeführt worden sind, und sie unterstützen die Hypothese der Nischenexpansion in mediterranen Gebieten. Sie bekräftigen aber nicht die Ergebnisse von anderen Autoren, nach denen eine Präferenz dieser Art für urbane Gebiete vorliegt.

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Changes in size, status, and distribution of badger *Meles meles* L. setts during a 20-year period

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Abstract

The size, status (whether "main setts" or "outliers"), and distribution of badger setts were compared using data from two separate surveys, begun in 1970 and 1990 respectively, of a 22 km^2 area in the south of England. During the period separating the two surveys, 24 main setts and 11 outliers persisted without a change of status; 1 main sett became an outlier and 14 outliers became main setts; 32 main setts and 131 outliers appeared de novo; and 5 main setts and 10 outliers disappeared. Main setts that persisted grew in size at an average rate of about 0.5 entrances per year. Changes in the status of a sett were not related to its initial size or habitat characteristics, but habitat changes or human interference were implicated in all cases in which main setts disappeared. Total number of main setts increased from 30 to 70, average territory size decreased from 0.7 km^2 to 0.3 km^2 and the number of outliers per territory increased from 1.2 to 2.0. The results suggest that when a badger population expands, new main setts are sometimes formed from existing outliers but are more often constructed de novo. Sometimes a main sett commanding a large territory is replaced by several new main setts and the territory is subdivided; on other occasions the original main sett persists and its territory is compressed as new territories are established in the vicinity.

Key words: *Meles meles*, mammal, burrow, distribution, territory

Introduction

Like many mammals (see review by Reichman and Smith 1990), badgers *Meles meles* L. are semi-fossorial: they are active on the surface at night, but sleep during the day in communal burrows known as "setts" (Neal 1977). The permanent place of residence of each social group is typically a single "main sett", distinguished by the fact that it is the largest burrow in the territory, is continuously occupied, and is used for breeding and overwintering (Neal 1977; Kruuk 1978; Roper and Christian 1992). Main setts are a traditional resource, handed on from generation to generation within a social group, as a consequence of which they can be continuously occupied for decades or even centuries (Neal and Roper 1991). Since successive occupants of a sett continue to enlarge it, ancient main setts can become extremely extensive: for example, Roper et al. (1991) describe a main sett of unknown age that possessed an estimated 50 nest chambers, 178 entrances and 879 m of underground tunnels (see Roper 1992 for other examples).

In addition to providing themselves with a main sett, badgers also often possess a number of smaller setts or "outliers", which are scattered around the territory and are only intermittently occupied (Kruuk 1978, 1989). These setts vary considerably in size: they can have from one to a dozen or more entrances and differ to a corresponding degree in the length of the underground tunnel network and the number of nest chambers

that they contain (e. g., ROPER 1992; ROPER et al. 1992). Thus badgers are remarkable amongst burrowing mammals for both the total amount and the diversity of underground space with which they provide themselves.

Although it is generally agreed that the size of a main sett is an indication more of its age than of the number of animals inhabiting it (KRUUK 1978; NEAL 1986; NEAL and ROPER 1991), there are no data available on the rate at which main setts increase in size over time. In addition, although it is relatively clear how the possession of an adequate main sett contributes to survival and reproduction in the animals occupying it (NEAL and ROPER 1991; ROPER 1992), it is less obvious why a social group of badgers that already possesses a main sett should also require one or more outliers within its territory. One possibility is that main setts and outliers constitute substitutable reservoirs of underground space, such that the possession of outliers compensates for a main sett that is relatively small in size and cannot be extended any further (OSTLER 1994). In this case, there should be an inverse correlation between the size of a main sett and the number of outliers that the corresponding territory contains. Another possibility is that as a badger population expands and new social groups form, outliers may become converted into main setts (NEAL and CHEESEMAN 1996). In this case, we would expect to see setts changing their status during the course of time.

Our study aimed to test these predictions by examining changes in the size, status, and distribution of individually identifiable main and outlier setts over time. We compared data from two detailed sett surveys of the same 22 km^2 area, undertaken in the early 1970's and the early 1990's respectively. As well as determining the size and characteristics of all setts within the area, we estimated territory boundaries using the method of Dirichlet tesselations (UPTON and FINGLETON 1985; DONCASTER and WOODROFFE 1993). This enabled us to examine the distribution of outliers across individual territories and also to visualise changes in territory size and shape that occurred as a consequence of new main setts becoming established.

Material and methods

Survey methods

The survey area covered 22.4 km^2 of contiguous South Downs farmland (see ROPER et al. 1995 for further details). The site was surrounded on all sides by busy roads but, other than farm tracks for occasional vehicles, it was devoid of any attenuating or dividing topographical features such as roads, rivers or walls. Stopping of setts by fox hunters (LINDSAY and MACDONALD 1985) was not practised in the area and in general, human interference was negligible except for agricultural activities.

The first of the two surveys was undertaken by E. D. CLEMENTS in May, June, August, and October of 1971, 1972, and 1974 (see CLEMENTS 1974; CLEMENTS et al. 1988 for details). Locations of setts were marked onto 1 : 25 000 scale maps and information about type of sett, number of entrances, type of surrounding habitat (e. g., unimproved grassland, woodland etc.) and presence or absence of cover was noted down in the field and subsequently transferred to index cards. Entrances were classified as "used" if they were free of debris such as sticks or leaves. The second survey was carried out by J. R. O. during November–February 1991/1992 and 1992/1993 and followed, as far as possible, the procedures described by CLEMENTS (1974).

When analysing the two sets of survey data, care was taken to use the same criteria for classifying setts and habitat types. Setts were classified as "main setts" or "outliers" according to Mammal Society guidelines (HARRIS et al. 1989; CRESSWELL et al. 1990). We did not subdivide outliers into the separate categories of "subsidiary setts" and "annexes" (KRUUK 1978; THORNTON 1988), since the distinctions between these are arbitrary and to a large extent subjective (NEAL and ROPER 1991). Thus, we use the term "outlier" to refer to any sett that was not a main sett.

Comparing results from the two surveys for purposes of analysis, it was possible to identify four possible outcomes as regards any one sett: a) a sett could persist from 1970 to 1990 without a change of status, i. e., a main sett could remain as a main sett, an outlier as an outlier; b) a sett could persist from

1970 to 1990 but change its status, from main sett to outlier, or vice versa; c) a sett could be new, i. e., have arisen de novo since the 1970 survey; d) a sett could have disappeared, i. e., be present in the 1970 survey but not in the 1990 survey. Setts were classified as having disappeared if no trace of them could be found despite thorough searching of the relevant area, or if nothing remained of the sett except overgrown and flattened spoil heaps, or entrances that were overgrown and completely blocked with soil, indicating that they had been abandoned for some years.

For purposes of analysis, we used total number of entrances as a measure of sett size. Data from excavated setts show that the number of entrances correlates well with other indices of sett size such as the area occupied by the underground tunnel system, the total length of tunnels, and the number of nest chambers (ROPER 1992).

Use of Dirichlet tesselations to estimate territory boundaries

Dirichlet tesselations provide a method of spatial analysis by which a pattern of points (in this case, locations of main setts) can be described in terms of the positions of each individual point relative to the positions of its immediate neighbours (UPTON and FINGLETON 1985). The method assumes that territory boundaries occur half way between adjacent pairs of setts and are oriented orthogonally to a line joining the two setts. When used to generate hypothetical congruent polygonal territory boundaries, the tesselations correspond reasonably well with real territory boundaries determined by bait-marking or radiotracking (DONCASTER and WOODROFFE 1993; OSTLER 1994).

Results

Inter-observer reliability

Since an element of subjectivity inevitably entered when sett entrances were classified as used or unused, it was necessary to compare the two surveys for inter-observer reliability. To do this we plotted the number of used entrances against the total number of entrances for 24 main setts for which data were available in both surveys. We predicted that if the same criteria were being used by both observers to classify entrances as "used", the ratio of used to total entrances should be the same for both datasets. This prediction was supported: the regression lines yielded by data from the two surveys were not significantly different in either slope ($T = 0.756$, $p = 0.453$) or intercept ($T = -1.352$, $p = 0.183$).

Setts persisting from 1970 to 1990 without a change of status

Twenty-four main setts and 11 outliers maintained their status over the 20-year period (Tab. 1). The main setts increased in size between 1970 and 1990 (Wilcoxon test, $Z = 3.17$, $N = 24$, $p < 0.01$), growing on average by about one new entrance every two years (see Tab. 2). There was no significant difference in the number of used entrances per main sett in 1970, by comparison with the number in 1990 (Wilcoxon test, $Z = -0.32$, $N = 25$, $p = 0.74$). However, there was a significant correlation between total number of entrances and number of used entrances in both surveys (Spearman test; 1970 data: $r_S = 0.39$, $N = 24$, $p = 0.056$; 1990 data: $r_S = 0.58$, $N = 24$, $p < 0.01$). Thus there was a tendency for larger setts to have more used entrances, but the number of used entrances did not grow in direct proportion to sett size.

There was no significant correlation between main sett size in 1970 and 1990 (Spearman test, $r_s = 0.24$, $N = 24$, $p = 0.26$), indicating that the rate of growth of main setts was not proportional to their original size. Nor was the percentage change in number of entrances related to the presence or absence of cover (Mann-Whitney test, $W = 113$, $N1 = 7$, $N2 = 11$, $p = 0.47$), indicating that open and covered setts grew in size at about the same rate. However, there was a just significant correlation between number of used entrances in 1970 and in 1990 (Spearman test, $r_s = 0.40$, $N = 24$, $p = 0.05$), suggesting that main setts that were relatively extensively occupied in 1970 continued to be so two decades later.

Table 1. Number ot setts with a given status in each of the two surveys. M denotes main sett, O denotes outlier, – denotes that the sett was absent at the time of the survey.

Status in 1970	Status in 1990	Number of setts	Description
M	M	24	Persisted as main sett
O	O	11	Persisted as outlier
M	O	1	Main sett → outlier
O	M	14	Outlier → main sett
–	M	32	New main sett
–	O	131	New outlier
M	–	5	Main sett which disappeared
O	–	10	Outlier which disappeared

Table 2. Number of entrances (mean and s. d.) at main setts in each of the two surveys.

Measure	Mean		Significance
	1970	1990	
Total entrances	15.9 (8.1)	26.5 (12.7)	$p < 0.01$
Used entrances	5.4 (2.6)	6.0 (3.7)	$p = 0.62$
% used entrances	38.0 (16.0)	24.9 (15.8)	$p = 0.01$

The 11 outliers that persisted from 1970 to 1990 did not change significantly in size (Wilcoxon test, $Z = -0.97$, $N = 11$, $p = 0.33$) or in number of used entrances ($Z = -1.19$, $N = 1$, $p = 0.23$).

Setts persisting from 1970 to 1990 but changing in status

Only one sett changed status from main sett to outlier and no habitat change was involved: the site remained without cover during the 20-year period. The 14 outliers that changed into main setts (Tab. 1) showed no significant difference in size or usage in 1970 when compared with 11 outliers which persisted over the 20-year period without changing status (total number of entrances: Mann-Whitney test, $W = 201$, $N1 = 11$, $N2 = 14$, $p = 0.31$; number of used entrances: $W = 207$, $N1 = 11$, $N2 = 14$, $p = 0.17$). That is, outliers which became main setts by 1990 were originally no larger or smaller than those which remained outliers. No habitat change was evident in any of the 14 cases: 10 setts remained in cover while 4 remained without cover. Outliers that changed status were no more or less likely to be in cover, or in the open, than outliers that persisted (χ_2=0.76, $df = 1$, $p = 0.38$).

New setts

Thirty two main setts and 131 outliers arose de novo since the 1970 survey (Tab. 1). The new main setts were significantly smaller in 1990 than main setts which persisted from 1970 (Mann-Whitney test, $W = 742$, $N1 = 24$, $N2 = 32$, $p < 0.01$) but they did not have a significantly different number of used entrances (Mann-Whitney test, $W = 870$, $N1 = 24$, $N2 = 32$, $p = 0.49$).

Of the 32 new main setts, 17 were in cover and 15 on open downland; of the 131 new outliers, 63 were in cover and 68 in the open.

Setts which disappeared

Five of the main setts that were identified in 1970 could not be found in the 1990 survey (Tab. 1). There was no significant difference in size or usage in 1970 between the five setts that subsequently disappeared and the other 24 main setts that persisted (Mann-Whitney test; total entrances: $W = 79.5$, $N1 = 5$, $N2 = 24$, $p = 0.82$; used entrances: $W = 76.5$, $N1 = 5$,

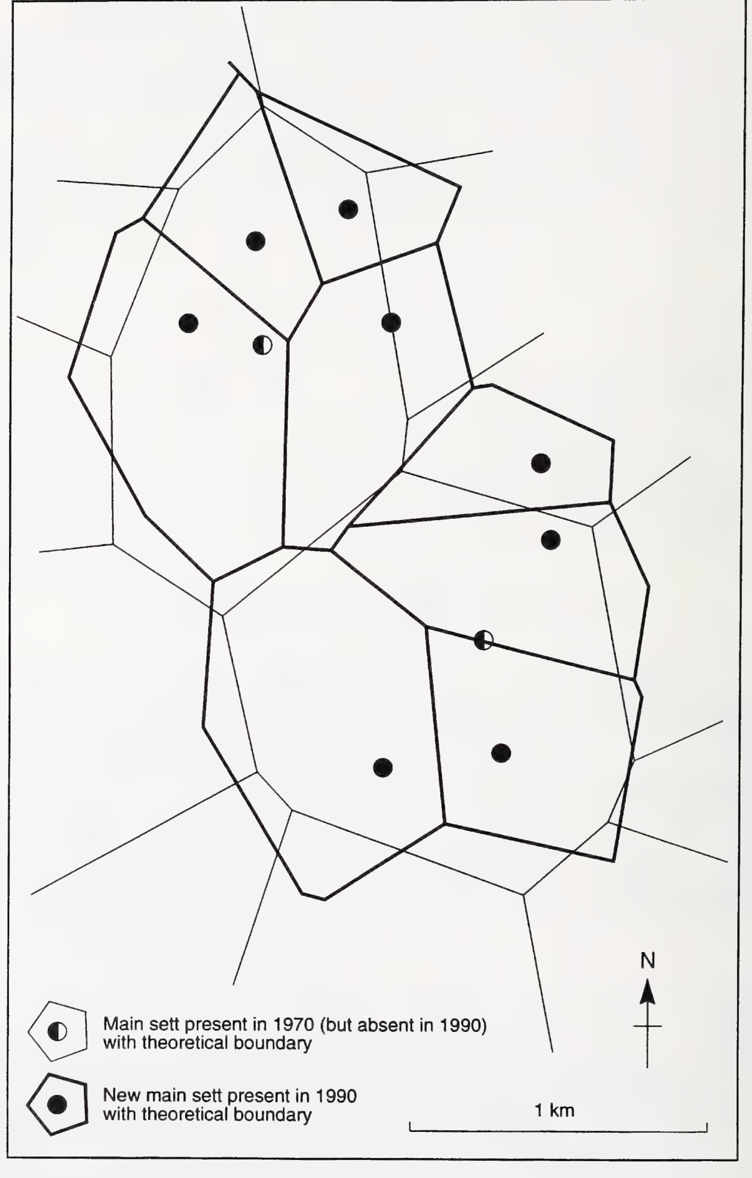


Fig. 1 a

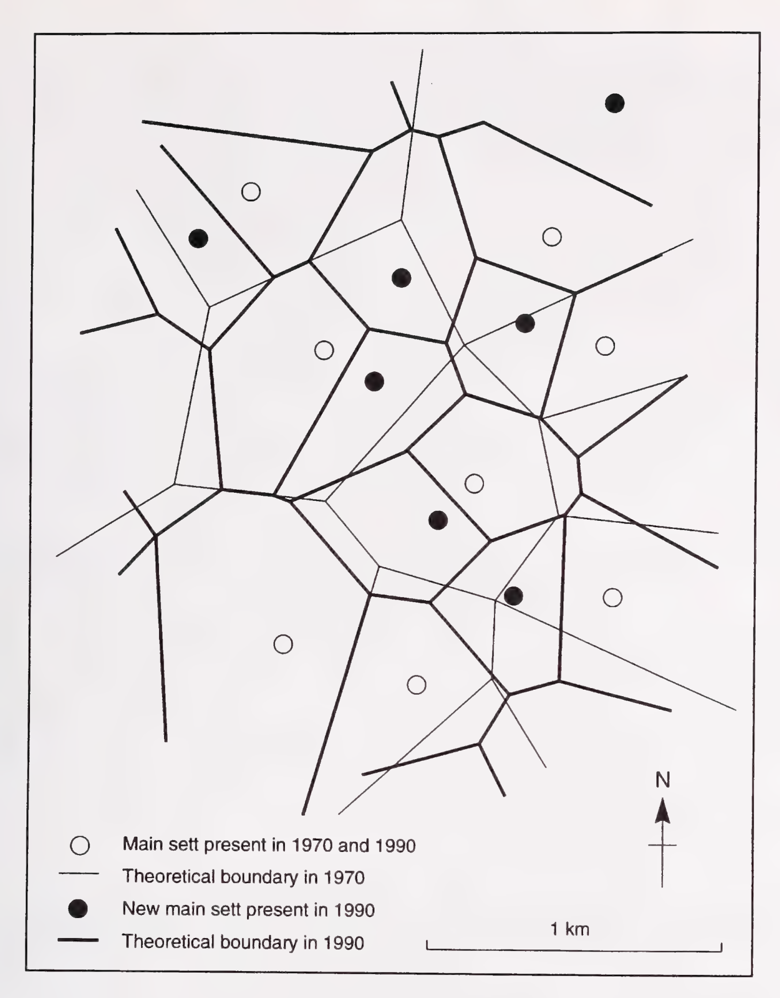


Fig. 1. Main sett locations and corresponding territory boundaries, estimated using Dirichlet tesselation. Thin lines: territory boundaries in 1970; thick lines: territory boundaries in 1990. (a) Cases in which main setts disappeared and the corresponding large territories were subdivided. Half-filled circles: main setts present in 1970 but absent in 1990; filled circles: main setts absent in 1970 but present in 1990. (b) Cases in which main setts persisted but new setts were established nearby, causing the original territories to shrink in size. Open circles: main setts present in both 1970 and 1990; filled circles: main setts absent in 1970 but present in 1990.

N2 = 24, p = 0.95). In four of the five cases, disappearance of the sett was attributable to habitat change (conversion of permanent pasture or scrub to arable). In the remaining case, the main sett was in a small wood close to a housing estate. It is probable that disturbance by humans caused this sett to be abandoned since the 1990 survey revealed a new main sett in a less accessible part of the same wood.

The 10 outliers which disappeared (Tab. 1) were not significantly different in terms of size or usage in 1970 when compared with outliers that persisted to 1990 (Mann-Whitney test; total entrances: W = 110.5, N1 = 10, N2 = 11, p = 1.00; used entrances: W = 129.5, N1 = 10, N2 = 11, p = 0.17). In only one of these cases, where open grassland had been converted to arable, was a habitat change implicated.

Changes in territories

When territories were visualised as Dirichlet tesselations, two types of change in territory conformation were evident as a consequence of the appearance of new main setts. In some cases, a main sett commanding a large territory in 1970 had disappeared by 1990 and the original large territory had become divided into several smaller territories, each occupied by a new main sett. Figure 1 a shows two examples of this process, in which two large territories lost their original main setts and apparently became divided into three or four smaller territories. In other cases the original main sett survived but new main setts were established nearby, causing the original large territory to be compressed by the appearance of new adjacent territories. Where this type of change occurred, it resulted in radical restructuring of the pattern of territorial boundaries (Fig. 1 b).

Combining data from both surveys, the number of outliers per territory varied from 0 to 9, with a mode of zero (Tab. 3). Over the range 0 to 4 outliers per territory, this was not significantly different from what would be expected by a random (Poisson) distribution ($\chi^2 = 4.04$, df = 3, p = 0.25). With 5, 6 or 7 outliers per territory, sample sizes were too small to test for a difference between the actual and expected distributions.

Table 3. Frequency distribution of number of outliers per territory, and number that would be expected by a Poisson distribution.

	0	1	2	3	4	5	6	7
Observed	39	26	12	11	4	0	1	1
Expected	45	31	13	4	1	0	0	0

Discussion

Several previous sett surveys have been undertaken in the UK (Neal 1972; Clements 1974; Clements et al. 1988; Thornton 1988; Cresswell et al. 1990; Feore et al. 1993; Smal 1993) including one in which a restricted area was resurveyed after a 20-year interval (Skinner et al. 1991 a, b). The aim of these surveys has been to provide estimates of badger population density in different parts of the UK at different times and to determine the geological and physiogeographical factors affecting sett distribution. The purpose of the present study, by contrast, was to provide detailed information about the fate of individual setts and territories over a 20-year period, within a relatively restricted but comprehensively surveyed area. During the 20-year period the number of main setts more than doubled, with a consequent reduction in average territory size from 0.7 km^2 to 0.3 km^2. Assuming an average of 5.9 adults per social group (Cresswell et al. 1990), this suggests that the population density of badgers increased from 7.97 adults/km^2 to 19.0 adults/km^2.

In assessing these results, it is important to ask to what extent the two surveys were comparable. Although care was taken to use the same methods in the second survey as in the first, the second took more time overall and was conducted in winter, when vegetation is less likely to have obscured sett entrances. The first survey may therefore have underestimated the number of outliers, since these are easily overlooked, especially when they have only one or two entrances. However, it is unlikely that either survey failed to detect main setts, which are usually easy to see in the open landscape of the chalk downland. In addition, the fact that "new" main setts (that is, main setts recorded in the second survey but not in the first) had significantly fewer entrances than "old" ones (that is, main

setts recorded in both surveys) is consistent with the assumption that they came into existence relatively recently. In addition, the fact that data from both surveys yielded a similar relationship between total number of entrances and number of used entrances suggests that the two surveys were using similar criteria to measure these variables. Finally, our results are consistent with the large increases in badger population size that have been recorded during the last two decades in other parts of the UK, using capture-recapture data (da Silva et al. 1993; Neal and Cheeseman 1996).

Five main setts (17% of those present in 1970) were lost between the two surveys. Four of these setts were ploughed up and one was probably subject to human interference from a nearby housing estate. This is consistent with the view that main setts are rarely abandoned except in circumstances of extreme disturbance (e. g., Neal 1977; Neal and Roper 1991). Main setts that persisted grew in size, though they did so at the surprisingly slow rate of about one new entrance every two years. This rate did not differ according to the initial size of the sett or to the presence or absence of cover, so it may be consistent enough to provide a rough means of estimating the age of a sett. However, the rate at which new entrances are dug is likely to vary with soil type and to be higher in new setts than in well established ones (Neal pers. comm.).

The fate of outliers was less predictable than that of main setts: of 35 outliers recorded in 1970, only 11 persisted while 10 disappeared and 14 became main setts. Thus main setts do sometimes arise by enlargement of existing outliers but they are more often dug de novo. The outliers that became main setts were no different in size from outliers that persisted or disappeared, nor were they more or less likely to be in cover, so the reason for their choice as future main setts remains obscure: one possibility is that they were located in more easily dug soil.

The modal number of outliers per territory was zero and the mean was only 1.97, which is slightly less than the mean for the UK as a whole of 2.8 outliers per main sett (Cresswell et al. 1989). There was no correlation between the size of a main sett and the number of outliers in the corresponding territory, suggesting that outliers are not a substitute for an inadequately sized main sett (Neal and Roper 1991). Outliers are sometimes used as temporary nocturnal resting places (Kruuk 1989), as daytime sleeping places in the summer (Roper and Christian 1992), as temporary accommodation for dispersing individuals (Christian 1994), as emergency refuges when an animal is threatened (Butler and Roper 1994), or occasionally for breeding (Neal and Cheeseman 1996). However, the existence of outliers is evidently not essential to the continued survival of a social group, since 40% of territories in our study area were found to lack them.

When territory boundaries were estimated using the method of Dirichlet tesselation (Doncaster and Woodroffe 1993) they suggested two patterns of realignment of boundaries consequent upon the appearance of new main setts. In some cases, the territory around an existing main sett became compressed as new main setts and their associated territories were established in the vicinity. In other cases, a main sett which had commanded a large territory disappeared, and the original large territory became subdivided into smaller territories, each with a new main sett. Cases of the latter type indicate that destruction of a main sett, for example by agricultural activities, can result in the fragmentation of social groups and the establishment of new territories.

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Zusammenfassung

Veränderungen in der Größe, dem Status und der Verteilung von Dachsbauen (Meles meles L.) über einen Zeitraum von 20 Jahren.

Die Resultate aus zwei Bestandsaufnahmen (1970 und 1990) zur Größe, zum Status (Hauptbau, Nebenbau) und zur Verteilung von Dachsbauen in einem 22 km^2 großen Gebiet in Südengland wurden verglichen. Den Zeitraum zwischen den Bestandsaufnahmen haben 24 Hauptbaue und 11 Nebenbaue ohne Statuswechsel überdauert, 1 Hauptbau wurde Nebenbau, und 14 Nebenbaue wurden zu Hauptbauen, 32 Hauptbaue und 131 Nebenbaue sind neu enstanden, und 5 Hauptbaue und 10 Nebenbaue sind verschwunden. Hauptbaue, die überdauert haben, sind im Durchschnitt um 1 Eingang pro 2 Jahre gewachsen. Veränderungen im Status eines Baues hingen nicht mit seiner ursprünglichen Größe zusammen oder mit Charakteristika des umgebenden Habitats, aber Habitatsveränderungen oder Störungen durch Menschen schienen in allen Fällen, in denen Hauptbaue verschwanden, eine Rolle gespielt zu haben.

Die Gesamtzahl an Hauptbauen stieg zwischen 1970 und 1990 von 30 auf 70 Hauptbaue, die durchschnittliche Territoriumsgröße fiel von 0,7 km^2 auf 0,3 km^2, die Anzahl Nebenbaue pro Territorium stieg von 1,2 auf 2,0. Wenn eine Dachspopulation wächst, scheinen diesen Ergebnissen zufolge neue Hauptbaue manchmal aus alten Nebenbauen zu entstehen, am häufigsten werden sie gänzlich neu angelegt. Manchmal wird ein Hauptbau in einem großen Territorium von mehreren neuen Hauptbauen abgelöst und das Territorium aufgeteilt; in anderen Fällen überdauert der alte Hauptbau und das zugehörige Territorium schrumpft zusammen, während sich in der Nachbarschaft neue Territorien bilden.

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Multivariate morphometrische Analysen der Gattung *Ovis* Linnaeus, 1758 (Mammalia, Caprinae)

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Abstract

Multivariate morphometric analysis of the genus Ovis Linnaeus, 1758 (Mammalia, Caprinae)

So far, univariate analyses were used exclusively to analyse the morphological variability of the genus *Ovis.* In contrast to these investigations 17 different measurements of the skull of 130 adult male specimens were analysed with multivariate methods in this study. The morphological similarities of the different forms were investigated using cluster analysis and canonical discriminant analysis. In contrast to results of univariate analyses we found clear differences between *O. ammon*, *O. canadensis*, *O. dalli*, *O. musimon*, and *O. nivicola*. Both cluster analysis and canonical discriminant analysis demonstrated that *O. nivicola* is morphologically more similar to the North-American forms *O. canadensis* and *O. dalli* than to each of the other Eurasian species. The results supported previous phylogenetic relationships based on cytogenetic analysis for the following forms: *O. ammon*, *O. canadensis*, *O. dalli*, *O. musimon* and *O. nivicola*. The cluster of the *O. vignei* and *O. orientalis* overlaid. Due to the small morphological variability between *O. vignei* and *O. orientalis* we conclude that these forms are sub-populations of one species.

Key words: *Ovis*, cluster analysis, discriminant analysis

Einleitung

Die Phylogenie der Gattung *Ovis* wird kontrovers diskutiert (Niethammer und Krapp 1986; Corbet und Hill 1987; Grubb 1990). Die Anzahl der Arten schwankt zwischen einer (Haltenorth 1963) und sieben (Honacki et al. 1982; Corbet und Hill 1987). Die These einer „Großart" wird durch den Nachweis von fertilen Hybriden gestützt (Nadler et al. 1971, Gray 1972). Auf der Basis unterschiedlicher Chromosomenzahlen (Nadler et al. 1973; Korobitsyna et al. 1974; Valdez et al. 1978) und der geographischen Verbreitung der einzelnen Formen werden hingegen folgende Einteilungen getroffen: 1) die mufflonartigen Schafe (*O. musimon* und *O. orientalis*, 2 n = 54) vorkommend in Europa, im Iran und dem Nahen Osten, 2) die Urialschafe (*O. vignei*, 2 n = 58) verbreitet im nordöstlichen Iran, in Mittelasien, Tadshikistan und Afghanistan, 3) die in den zentralasiatischen Gebirgslandschaften lebenden argaliartigen Schafe (*O. ammon*, 2 n = 56), 4) das sibirische Schneeschaf (*O. nivicola*, 2 n = 52) kommt auf der Halbinsel Kamtschatka sowie in Nord- und Nordostsibirien vor sowie 5) die nordamerikanischen Formen (*O. canadensis*, *O. dalli*, 2 n = 54) (Corbet und Hill 1987; Grubb 1990). Shackleton und Lovari (1997) fassen *O. musimon*, *O. orientalis* und *O. vignei* unter *O. orientalis* zusam-

men. *O. musimon* wird auch als eigenständige Art, als Synonym für *O. ammon* oder als im Neolithikum verwilderte Hausschafform geführt (Röhrs 1986).

Eine Klassifizierung basierend allein auf Unterschieden in der Chromosomenzahl ist kritisch zu betrachten, da die Wildschafe zueinander im Verhältnis eines Robertsonschen Polymorphismus stehen. Weiterhin stimmen die G-Bandenmuster und Meiosebilder von Hybriden nordamerikanischer und europäischer Wildschafe überein (Niethammer und Krapp 1986).

Untersuchungen zur morphologischen Variabilität umfaßten bisher nur univariate Vergleiche. Eine deutliche Abgrenzung der Arten durch bestimmte Proportionen wurde dabei nicht erreicht (Oehmischen 1923; Kesper 1953). Das Ziel der durchgeführten Analysen bestand in der Erfassung der morphologischen Variabilität. Den Nachteilen eines Vergleichs nur einzelner Merkmale wurden multivariate Analysen gegenübergestellt.

Material und Methode

Es wurden Wildschafschädel aus folgenden Sammlungen untersucht: Museum für Naturkunde der Humboldt-Universität Berlin, der Julius-Kühn-Sammlung der Landwirtschaftlichen Fakultät der Universität Halle/Sa., dem Tierkundemuseum Dresden und der Zoologischen Staatssammlung München.

Es wurden folgende 17 Schädelmaße von 130 adulten männlichen Individuen mit dem Tasterzirkel bzw. Meßschieber abgenommen (Abb. 1):

W1 = Condylobasallänge: Hinterrand der Condyli occipitales – Prosthion
W2 = Basion – Prosthion (Basallänge)
W3 = Basion – Prämolare (Kleine Schädellänge)
W4 = Prämolare – Prosthion
W5 = Nasion – Prosthion (Gesichtsschädellänge)
W6 = Akrokranion – Nasion (Mediane Stirnlänge)
W7 = Akrokranion – Supraorbitale (Obere Hirnschädellänge)
W8 = Supraorbitale – Prosthion (Gesichtslänge)
W9 = Endorbitale – Prosthion (Orbitalabstand)
W10 = Nasion – Rhinion (Größte Länge des Nasenbeins)
W11 = Postdentale – Prosthion (Dentallänge)
W12 = Alveolenmaß gleich Länge der Backzahnreihe
W13 = Größte Innenhöhe einer Orbita
W14 = Laterale Länge des Os incisivum: Abstand zwischen Nasointermaxillare und Prostion
W15 = Kleinste Breite der Facies parietalis gleich Parietalbreite: zwischen den stärksten Einziehungen der Lineae temporales
W 16 = Größte Breite über den Orbitae = Stirnbreite = größte Breite des Schädels: Ectorbitale – Ectorbitale
W17 = Breite über den Tubera malaria (Wangenbreite)

Alle Maße wurden dreimal abgenommen und die arithmetischen Mittelwerte für die statistische Auswertung gebildet.

Die Auswertung der ermittelten Daten erfolgte mit Hilfe der Verfahren der Clusteranalyse und der Canonischen Diskriminanzanalyse. Die Clusteranalyse nach Ward ist ein numerisches Verfahren zur Strukturanalyse von Datenmengen, bei denen das Ergebnis nicht durch Vorgaben (Klasseneinteilung) beeinflußt wird (Deichsel und Trampisch 1985). Jedes Objekt bildet anfänglich ein Cluster, danach wird die Anzahl der Cluster reduziert, indem die beiden ähnlichsten vereinigt werden. Dieses Verfahren diente zur Selektion der Klassen für die Canonische Diskriminanzanalyse. Die vorgegebenen Klassen entsprachen der Einteilung nach Nadler et al. (1973). Die Canonische Diskriminanzanalyse berechnet die Unterschiede zwischen den einzelnen Klassen. Die Trennung erfolgt durch Erfassung einer Anzahl von Merkmalen an jedem einzelnen Element der Gesamtheiten und durch Aufstellen einer Trennfunktion, die über die Zuordnung der Elemente entscheidet und damit als Entscheidungsfunktion bezeichnet wird. Bei der Trennung von Individuen auf der Basis mehrerer Merkmale wird sich bei dieser Methode sogenannter Canonischer Faktoren (CAN 1 ... CAN n) bedient. Diese entsprechen line-

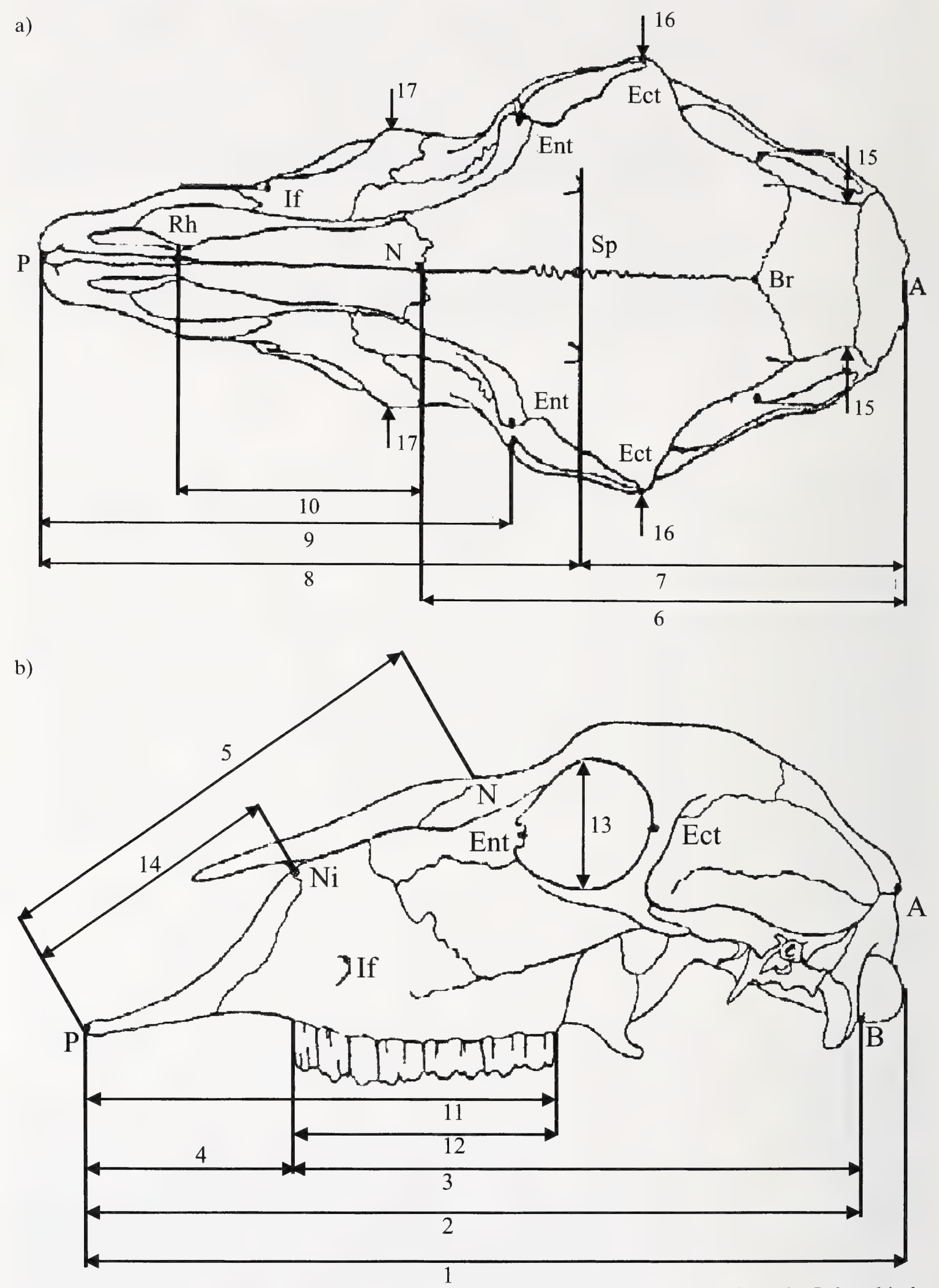


Abb. 1. a) Schädel von *Ovis* in der Ansicht von oben (P – Prosthion, Rh – Rhinion, If – Infraorbitale, N – Nasion, Ent – Entorbitale, Sp – Supraorbitale, Ect – Ectorbitale, Br – Bregma, A – Akrokranion), dargestellt sind die Maße W6–W10 und W15–W17. b) Schädel von *Ovis*, Seitenansicht (P – Prosthion, Ni – Nasointermaxilares, If – Infraorbitale, N – Nasion, Ent – Entorbitale, Ect – Ectorbitale, B – Basion, A – Akrokranion), abgebildet sind folgende Maße: W1–W5 und W11–W14. Die Darstellungen sind modifiziert nach BOESSNECK et al. (1964).

aren Kombinationen der quantitativen Variablen, wobei diejenigen für die Trennung verantwortlich sind, welche die größten Differenzen zwischen den Klassen darstellen. Es sind nicht die Einzelwerte, sondern die Mittelwerte der einzelnen Klassen entscheidend.

Der CAN 1 Faktor berechnet sich aus dem Merkmal m, welches der Größe nach innerhalb der untersuchten Individuen abgestuft wird. Es werden also b1×1 + b2×2 + ... + bm×m gebildet. Das heißt, um ein Element der Stichprobe 1 sind die Merkmale 1, 2, ... m gemessen, jeder Meßwert ×1, ×2 usw. wird mit einem Faktor b1, b2 ... bm multipliziert. Danach werden alle erhaltenen Werte der einzelnen Merkmale addiert.

Der CAN 2 Faktor steht in keiner Beziehung zu CAN 1. Er geht von einer hypothetischen Normalverteilung der Parameter aus. Bei der Berechnung des CAN 2 entfällt der Parameter, welcher für die Trennung entlang der ersten canonischen Achse verantwortlich ist. Es erfolgt eine erneute Berechnung der nicht korrelierenden Anteile unter Zugrundelegung der für den CAN 1 geltenden Formel.

Die Korrelationskoeffizienten nach Pearson, die Clusteranalyse und die Canonischen Diskriminanzanalysen wurden mittels des Programmpaketes SAS (SAS Inst. Inc., USA) durchgeführt.

Ergebnisse

Auf der Grundlage der ermittelten morphometrischen Parameter der untersuchten Wildschafschädel (Tab. 1) erfolgten die Clusteranalyse und die Canonischen Diskriminanzanalysen. Die Clusteranalyse (Abb. 2) aller Individuen ergab eine klare Abspaltung von *O. ammon*. Diese Form war über zwei Cluster (6 und 7) verteilt. Ein *O. ammon* gruppierte sich in das Cluster 4. *O. canadensis* belegte vorrangig das 5. Cluster, während sämtliche Tiere von *O. dalli* und *O. nivicola* im 4. Cluster vertreten waren. In den Clustern 1, 2 und 3 lagen *O. musimon*, *O. orientalis* sowie *O. vignei*. Dabei gab es vor allem starke Überschneidungen zwischen *O. vignei* und *O. orientalis*. *O. musimon* lag fast ausschließlich im 3. Cluster.

Wurden die ermittelten Daten aller 130 Schädel in die Diskriminanzanalyse einbezogen (Abb. 3), so ergaben sich Überschneidungen zwischen den einzelnen Wildschafformen. Der erste und zweite Canonische Faktor (CAN 1 und CAN 2) wurden am stärksten durch W10 und W17 beeinflußt. Für CAN 1 waren die Parameter W10 und W12 entscheidend, während der CAN 2 von W17 und W6 abhängig war. Es wurden drei große Gruppen unterschieden. Eine Gruppe bildeten *O. canadensis*, *O. dalli* und *O. nivicola*. *O. musimon*, *O. orientalis* und *O. vignei* sowie *O. ammon* gruppierten sich zu zwei weiteren Gruppen. Zwischen diesen Gruppen existierten teilweise Übergänge. Durch den CAN 2 wurden *O. dalli* und *O. nivicola* sowie teilweise *O. canadensis* abgetrennt. Die Aufspaltung der eurasischen Gruppen erfolgte durch den CAN 1 (Abb. 4). Es wurde eine klare Abspaltung der *O. ammon* erreicht. Zwei Tiere von *O. ammon* befanden sich deutlich außerhalb des Clusters dieser Form. Beide Individuen waren Zootiere mit unklarer Herkunft. Der CAN 2 trennte *O. musimon* von den anderen Formen. *O. orientalis* und *O. vignei* gruppierten sich zusammen. In Abb. 5 wurden *O. canadensis*, *O. dalli* und *O. nivicola* getrennt von den anderen Formen analysiert. Durch den CAN 1 wurden *O. canadensis* und *O. dalli* von *O. nivicola* abgespalten. *O. canadensis* und *O. dalli* wurden durch den CAN 2 getrennt. Sowohl die Clusterung nach Unterarten als auch nach Fundorten brachte keine weitere Differenzierung der untersuchten *O. ammon* und *O. nivicola*. Die Korrelationskoeffizienten zwischen den erfaßten Parametern sind in Tab. 2 dargestellt.

Diskussion

Phylogenie der Gattung *Ovis*

Übereinstimmend mit der Systematik von Grubb (1990), bzw. Corbet und Hill (1987) basierend auf den Untersuchungen von Nadler et al. (1973), Korobitsyna et al. (1974)

Tabelle 1. Minima und Maxima sowie Mittelwerte und Standardabweichungen der erfaßten Parameter (in mm) der untersuchten Individuen

Parameter	*O. ammon* (n = 44)	*O. canadensis* (n = 12)	*O. dalli* (n = 9)	*O. musimon* (n = 21)	*O. nivicola* (n = 7)	*O. orientalis* (n = 9)	*O. vignei* (n = 28)
W1	233–374 323,8 ± 33,22	275–322 302,7 ± 16,04	262–292 277,7 ± 9,54	201–244 229,4 ± 10,55	260–276 270,4 ± 5,86	201–262 240,8 ± 20,61	215–287 250,5 ± 17,66
W2	231–374 321,7 ± 34,98	275–320 300,7 ± 16,20	262–291 275,2 ± 9,18	201–241 227,7 ± 10,20	259–274 269,6 ± 5,53	201–259 238,8 ± 19,43	213–283 247,7 ± 17,31
W3	164–270 235,8 ± 23,54	201–239 220,7 ± 12,40	192–213 200,1 ± 6,97	153–179 170,8 ± 6,66	192–206 201,1 ± 6,04	156–197 179,8 ± 14,07	158–210 185,8 ± 12,41
W4	41–109 87,1 ± 12,21	74–94 82,8 ± 6,37	72–85 76,8 ± 4,47	48–67 57,9 ± 4,89	67–79 71,7 ± 4,75	45–74 59,9 ± 7,88	47–76 63,0 ± 6,78
W5	104–251 197,3 ± 30,19	153–187 175,6 ± 9,78	141–174 153,6 ± 9,70	106–147 126,7 ± 9,61	134–152 145,4 ± 6,63	111–149 136,8 ± 11,49	115–168 142,0 ± 13,35
W6	132–218 159,6 ± 14,74	141–178 159,4 ± 11,29	143–164 150,3 ± 7,76	112–132 123,8 ± 6,00	143–166 149,6 ± 7,91	99–140 127,4 ± 13,49	111–145 131,4 ± 9,13
W7	86–157 131,5 ± 16,76	107–139 126,0 ± 10,24	115–133 124,0 ± 6,02	84–107 94,1 ± 6,18	107–125 119,1 ± 6,47	83–111 99,6 ± 9,88	82–122 105,1 ± 10,87
W8	198–362 290,6 ± 35,64	246–298 261,0 ± 27,42	212–259 239,3 ± 14,97	165–211 194,4 ± 11,22	213–241 230,4 ± 9,74	178–220 208,2 ± 15,69	185–242 214,4 ± 15,61
W9	124–237 198,1 ± 23,38	171–198 183,5 ± 10,29	148–174 163,2 ± 7,43	113–139 129,0 ± 7,07	150–158 154,6 ± 2,94	113–153 139,1 ± 12,40	122–170 145,8 ± 12,62
W10	79–169 125,2 ± 19,10	85–121 109,7 ± 10,38	79–105 88,7 ± 9,18	67–108 84,0 ± 8,73	74–94 84,7 ± 7,67	74–93 87,9 ± 5,84	69–106 91,5 ± 8,76
W11	90–212 174,0 ± 20,86	155–179 166,9 ± 7,99	142–158 151,2 ± 4,76	105–136 126,1 ± 7,73	142–145 142,7 ± 2,14	104–147 129,3 ± 13,23	117–154 137,2 ± 8,78
W12	61–112 87,5 ± 10,38	76–90 83,8 ± 5,63	66–79 72,1 ± 3,98	56–86 67,4 ± 6,18	66–75 70,3 ± 3,35	57–74 68,0 ± 6,71	65–79 72,5 ± 3,68
W13	46–60 54,1 ± 3,26	47–54 50,2 ± 1,96	44–48 46,0 ± 1,22	38–45 42,4 ± 1,86	43–50 46,0 ± 2,08	39–49 44,8 ± 3,15	42–49 45,6 ± 1,66
W14	65–150 120,7 ± 17,50	75–108 96,9 ± 8,81	77–90 83,6 ± 4,10	58–80 69,3 ± 7,25	77–118 92,6 ± 12,92	52–92 78,8 ± 11,43	67–103 83,6 ± 10,48
W15	39–102 65,8 ± 15,18	47–76 60,3 ± 9,28	47–59 52,2 ± 4,09	36–54 45,2 ± 4,69	39–72 60,4 ± 11,89	40–57 47,2 ± 5,97	37–56 46,4 ± 4,73
W16	126–202 175,2 ± 17,91	148–180 168,9 ± 10,25	149–170 158,4 ± 7,25	108–132 120,9 ± 6,26	153–175 164,9 ± 8,86	107–136 126,7 ± 9,59	113–151 133,8 ± 9,37
W17	74–110 94,8 ± 9,93	81–107 94,1 ± 7,54	81–95 87,9 ± 5,09	59–74 69,2 ± 3,96	78–88 80,3 ± 8,60	58–81 73,1 ± 7,29	63–87 74,6 ± 5,79

und Valdez et al. (1978) und im Gegensatz zu Oehmischen (1923) und Kesper (1953) wurde eine klare Differenzierung der Formen *O. ammon*, *O. canadensis*, *O. dalli*, *O. musimon* und *O. nivicola* erreicht. Im Gegensatz zu Kesper (1953), welcher die eurasischen Wildschafe zu einer Art zusammenfaßte, unterstützen die in dieser Arbeit gefundenen morphologischen Unterschiede die Theorie von Nadler et al. (1973) und Honacki et al. (1982), daß *O. musimon* eine eigenständige Art darstellt. Die gefundenen hohen morphologischen Distanzen werden durch geologische Untersuchungen gestützt. Der letzte Landkontakt zwischen dem Festland und Korsika, bzw. Sardinien existierte vor ca. 5,3 Mio. Jahren (Schüle 1993). Trotz historischem sympatrischen Vorkommen von argaliartigen und mufflonartigen Wildschafen in Europa (Korobitsyna et al. 1974; Herre und

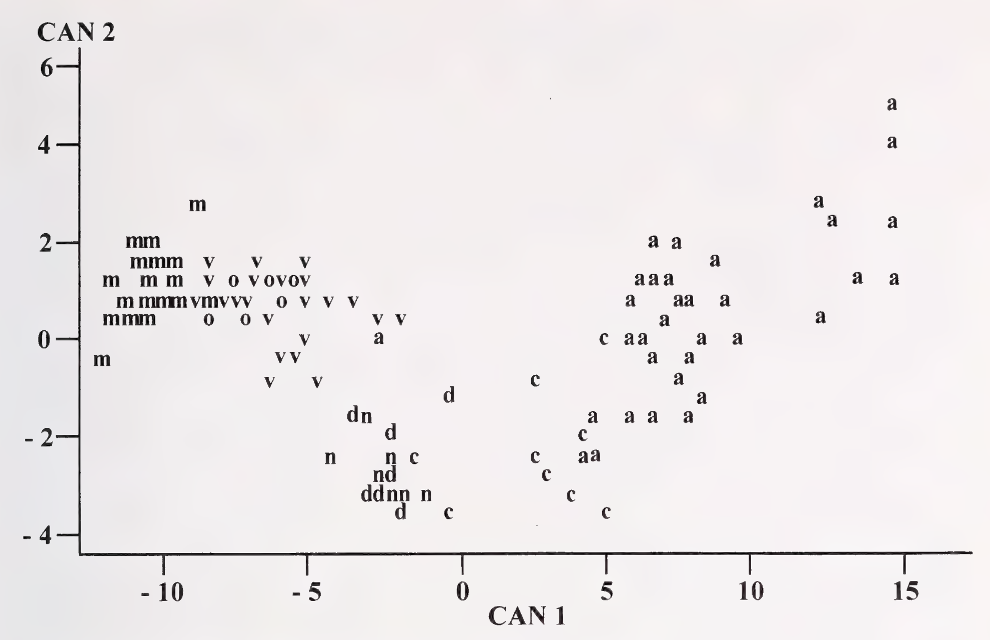


Abb. 2. Ergebnisse der Clusteranalyse der untersuchten adulten männlichen Individuen: a – *O. ammon*, c – *O. canadensis*, d – *O. dalli*, m – *O. musimon*, n – *O. nivicola*, o – *O. orientalis*, v – *O. vignei*).

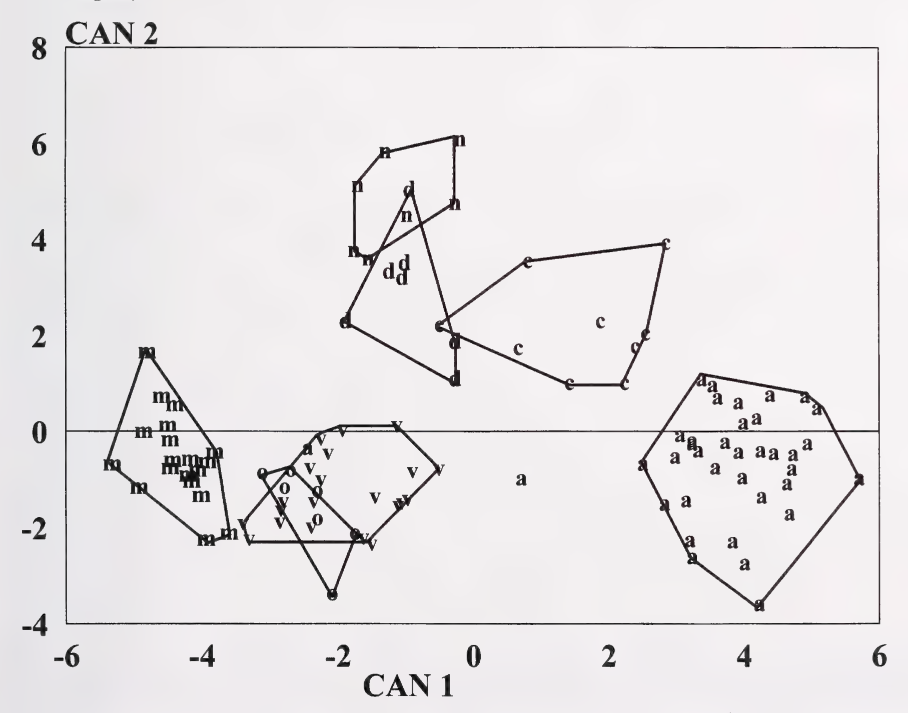


Abb. 3. Verteilung der untersuchten adulten männlichen Individuen (a – *Ovis ammon*, c – *O. canadensis*, d – *O. dalli*, m – *O. musimon*, n – *O. nivicola*, o – *O. orientalis*, v – *O. vignei*) entlang der ersten und zweiten Canonischen Achse.

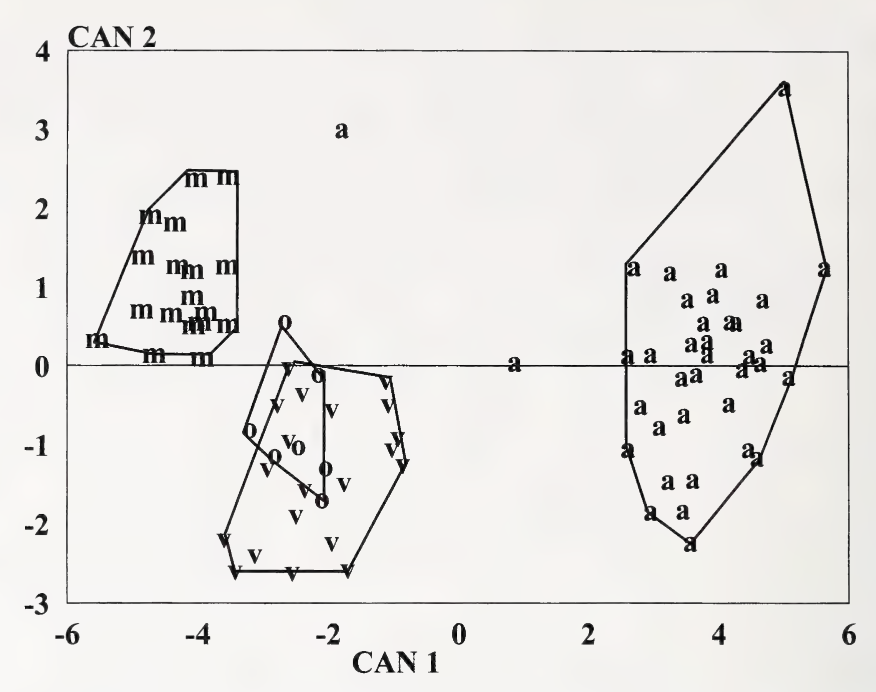


Abb. 4. Verteilung der untersuchten adulten männlichen Individuen (a – *Ovis ammon*, m – *O. musimon*, o – *O. orientalis*, v – *O. vignei*) entlang der ersten und zweiten Canonischen Achse.

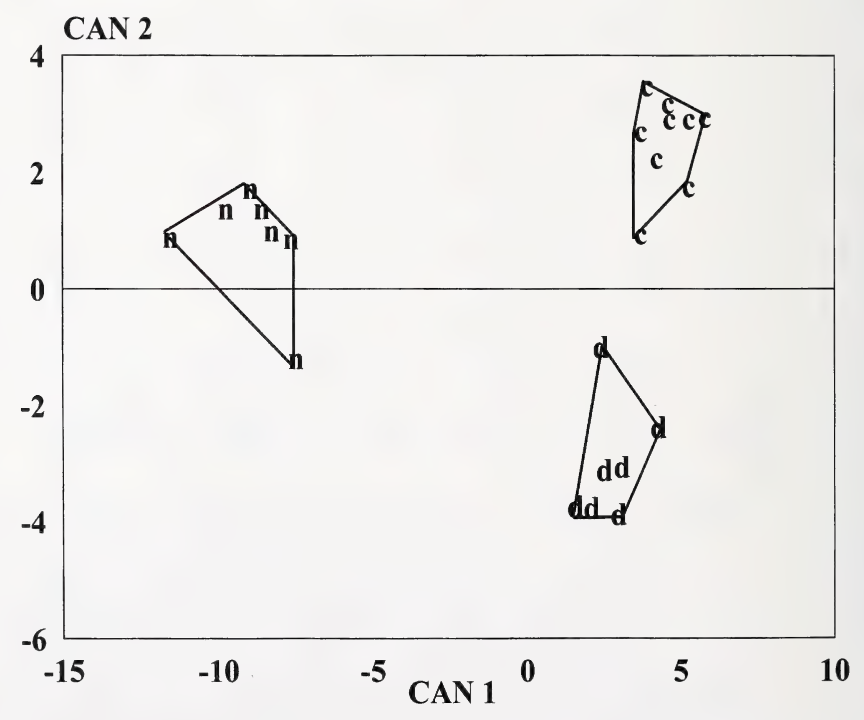


Abb. 5. Verteilung der untersuchten adulten männlichen Individuen (c – *Ovis canadensis*, d – *O. dalli*, n – *O. nivicola*) entlang der ersten und zweiten Canonischen Achse.

Tabelle 2. Korrelationskoeffizienten der untersuchten morphometrischen Parameter

Para-meter	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	W12	W13	W14	W15	W16	W17
W1	1,0	1,00	0,99	0,95	0,97	0,91	0,88	0,97	0,99	0,90	0,96	0,84	0,90	0,92	0,82	0,95	0,92
W2		1,0	0,99	0,96	0,97	0,91	0,87	0,97	0,99	0,90	0,96	0,84	0,90	0,92	0,83	0,95	0,92
W3			1,0	0,92	0,96	0,91	0,89	0,96	0,97	0,90	0,94	0,84	0,90	0,91	0,83	0,95	0,92
W4				1,0	0,92	0,85	0,80	0,92	0,96	0,82	0,95	0,77	0,83	0,89	0,75	0,90	0,86
W5					1,0	0,79	0,85	0,95	0,97	0,93	0,95	0,84	0,88	0,91	0,79	0,91	0,88
W6						1,0	0,85	0,87	0,88	0,75	0,85	0,73	0,80	0,80	0,77	0,90	0,87
W7							1,0	0,83	0,83	0,79	0,79	0,67	0,76	0,75	0,76	0,88	0,85
W8								1,0	0,97	0,89	0,93	0,82	0,89	0,90	0,83	0,93	0,91
W9									1,0	0,89	0,97	0,85	0,89	0,93	0,79	0,93	0,91
W10										1,0	0,86	0,81	0,84	0,85	0,78	0,84	0,82
W11											1,0	0,89	0,85	0,91	0,75	0,90	0,88
W12												1,0	0,78	0,80	0,64	0,78	0,79
W13													1,0	0,85	0,78	0,86	0,84
W14														1,0	0,74	0,87	0,82
W15															1,0	0,82	0,82
W16																1,0	0,92
W17																	1,0

Röhrs 1990) sprechen die gefundenen morphologischen Unterschiede für eine Trennung beider Formen. Petit et al. (1997) fanden bei genetischen Analysen an mediterranen Mufflons eine größere Variabilität als sie auf Grund des historischen Bottlenecks der *O. musimon* Populationen erwarteten. Möglicherweise ist diese Variabilität in Hybridisierungen begründet. Anderseits argumentieren Shakleton und Lovari (1997), daß die mufflonartigen Schafe durch den Menschen auf den mediterranen Inseln eingeführt wurden. Der Bottleneck der Haustierhaltung kann damit Grundlage für die nachgewiesenen morphologischen Differenzen sein. Die geographische Isolation der rezenten, autochthonen *O. musimon* auf Korsika und Sardinien kann gleichfalls eine Ursache sein.

Aufgrund der hohen morphologischen Ähnlichkeit von *O. orientalis* und *O. vignei*, ist der taxonomische Status dieser Formen kritisch zu betrachten. Es kann sich bei diesen Formen um Subpopulationen handeln. Eine klare Differenzierung wurde in Übereinstimmung mit Kesper (1953) zwischen *O. ammon* und den anderen Formen nachgewiesen. Eine Aufspaltung in vier Rassen unterstützen unsere Ergebnisse allerdings nicht, da in Cluster- und Diskriminanzanalyse eine homogene Gruppierung von *O. ammon* ermittelt wurde.

Die größere morphometrische Ähnlichkeit von *O. nivicola* zu den nordamerikanischen Formen als zu den eurasischen Wildschafen erklärt sich möglicherweise in der postglazialen Ausbreitung der Wildschafe. Nach der Besiedlung Nordamerikas durch die Wildschafe wurden diese in der folgenden Eiszeit vorübergehend nach Süden verdrängt und besiedelten dann Nordamerika und Sibirien neu (Thenius 1972; Shackleton 1985). Migrationsprozesse und Isolationsphasen, bedingt durch glaziale und interglaziale Barrieren, führten zur

Herausbildung der einzelnen Formen (KOROBITSYNA et al. 1974). Paleontologische und verhaltensbiologische Studien unterstützen diese Hypothese (GEIST 1971). Anderseits deuten Untersuchungen von Haplotypen mitochondrialer DNA von *O. canadensis* auf das Fehlen von zoogeographischen Barrieren hin (RAMEY 1995). Eine abschließende Klärung sollte mit der vergleichenden Analyse verschiedener Merkmalssysteme erreicht werden.

Eignung der Methode

In dieser Arbeit wurde versucht, die innerartliche Variabilität sowie die artspezifischen Unterschiede der Gattung *Ovis* darzustellen. Multivariate Vergleiche benötigen für solche Untersuchungen ein geringeres Datenmaterial als univariate Analysen. Ausschlaggebend dafür ist die höhere Trennschärfe multivariater Verfahren. Sie sollten somit geeignet sein, um Unterschiede aufzuzeigen, welche bei der traditionellen univariaten Betrachtung von untergeordneter Bedeutung sind (AHRENS und LÄUTER 1981). Die mehrdimensionale Diskriminanzanalyse ermöglichte eine geschlossene Übersicht über die in dem Datenmaterial verborgenen Zusammenhänge. Das Problem bei der Diskriminanzanalyse besteht in der Zuordnung der einzelnen Individuen zu den einzelnen Klassen. Eine Fehleinteilung der Klassen kann letztlich zu einer Fehlinterpretation der Ergebnisse führen. In dieser Arbeit erfolgte die Einteilung der Klassen auf der Basis der Trophäenausbildung (OEHMISCHEN 1923; KESPER 1953) und der vorangegangen Clusteranalyse. Ergänzend wurden die teilweise bekannten Fundorte der einzelnen Individuen überprüft. Es zeigte sich, daß die Diskriminanzanalyse kombiniert mit der Clusteranalyse ein leistungsfähiges Verfahren war, bei dem Differenzen sichtbar wurden, die im Vergleich zu bisher vorliegenden univariaten Tests nicht erfaßt wurden.

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Zusammenfassung

Untersucht wurde mittels Canonischer Diskriminanzanalyse und Clusteranalyse die morphologische Variabilität der Gattung *Ovis*. Es wurden 17 Maße des Schädels von 130 adulten männlichen Individuen abgenommen. Die Zuordnung der einzelnen Individuen zu den potentiellen Klassen für die Diskriminanzanalyse wurde mit Hilfe der Clusteranalyse, der Trophäenausbildung und des Fundortes überprüft. Im Gegensatz zu den bisher durchgeführten univariaten Analysen gelang eine klare Differenzierung der Formen *O. ammon*, *O. canadensis*, *O. dalli*, *O. musimon* und *O. nivicola*. Die Ergebnisse der Untersuchungen unterstützten die Klassifizierung auf der Basis von unterschiedlichen Chromosomenzahlen und geographischer Verbreitung für folgende Taxa: *O. ammon*, *O. canadensis*, *O. dalli*, *O. musimon* und *O. nivicola*. Die nachgewiesene hohe morphologische Ähnlichkeit zwischen *O. vignei* und *O. orientalis* spricht dafür, daß es Subpopulationen einer Art sind.

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Size-independent distribution of bronchial cartilage in four species of myomorph rodents

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Abstract

The size-independent distribution of bronchial cartilage in the conductive bronchial tree of four species of myomorph rodents different in body weight was determined by the inspection of translucent cartilage-stained whole-lung-specimens in comparison to bronchial casts. The lungs of the harvest mouse, *Micromys minutus*, body weight 5–7 g, the laboratory house mouse, *Mus musculus*, body weight 35–45 g, the laboratory brown rat, *Rattus norvegicus*, body weight 200–400 g, and the African giant pouched rat, *Cricetomys gambianus*, body weight 1 200–1 800 g, show the same lobulation and ramification of the conductive bronchial tree. All four rodents possess dorsally open cartilaginous braces in the trachea and in both main bronchi up to the first ventral branch of the left lung or to the emerging bronchus of the right middle lobe. The distribution of cartilage tissue in the bronchial tree of the four species investigated is identical and shows no relation to the size of the lung or the bronchi. The definition of the term "bronchus" by the presence of cartilage is criticized and the function of intrapulmonary bronchial elements is discussed.

Key words: Rodentia, lung, airways, bronchi, cartilage

Introduction

The generally assumed function of cartilage in any airway system is to keep the airways open and to prevent their collapse. In the literature the subject of the function of airway cartilage has been completely ignored. The present investigation determines the distribution of bronchial cartilage in the conductive bronchial tree of mammals of close phylogenetical relation, similar body proportions, comparable locomotory habits, and identical lung anatomy, differing mainly in their adult body size (Gehr et al. 1981). Previous studies of the author proved the four considered species to yield a good basis for this comparison. The lungs of *Micromys*, *Mus*, *Rattus*, and *Cricetomys* share all basic morphological parameters. The lung volumes of all four species are isometrical to their body weight. *Micromys*, *Mus*, *Rattus*, and *Cricetomys* all show an identical pattern of bronchial ramification and of lung lobulation (Valerius 1996). The influence of body size on the cartilaginous stiffening of the bronchi was expected to enlighten the functional relations under which these chondroid elements have evolved.

In compensation for the term "ring" the term "brace" or "C-shaped brace" is used in the present study for the larger extrapulmonary cartilaginous elements. According to the generally used nomenclature, smaller, irregular chondroid elements are called "plates" (Vanpeperstraete 1973).

Material and methods

From previous studies (VALERIUS 1996; DIETERLEN 1988), the biological data for the harvest mouse, *Micromys minutus* Pallas, 1771, the house mouse, *Mus musculus* Linnaeus, 1758, the brown rat, *Rattus norvegicus* Berkenhout, 1769, and the giant pouched rat, *Cricetomys gambianus* Waterhouse, 1840, are listed in table 1. The given mean values were taken from adult animals of both sexes. For a description of the method for preparing the silicon rubber casts, see VALERIUS (1996).

Table 1. Mean body weights, total body lengths and nose-rump lengths of *Micromys*, *Mus*, *Rattus*, and *Cricetomys*.

Species (n)	body weight	total body length	nose-rump-length
Micromys (15)	6.6 g	111 mm	56 mm
Mus (15)	35.9 g	198 mm	102 mm
Rattus (14)	255.9 g	394 mm	211 mm
Cricetomys (13)	1447.5 g	693 mm	357 mm

Micromys is one of the smallest mammals, whereas *Cricetomys* is a giant myomorph rodent and a medium-sized mammal. The lung sizes of all four species are compared in figure 1, the ramification of the bronchi in the left lung as represented by bronchial casts is shown in figure 2. *Micromys*, *Mus*, and *Rattus* are genera of the family Muridae, while the taxonomy of *Cricetomys* is subject to discussion. This animal may be placed either in the family of Cricetidae or in a separate family, the Cricetomyidae (DIETERLEN 1988). Its lung anatomy is in all regards similar to that of the other three species.



Fig. 1. Freeze-dried lungs of *Micromys* (A), *Mus* (B), *Rattus* (C), and *Cricetomys* (D), showing the identical lobulation and the size relations of the lungs in the ventral view. Scale bar represents 100 mm.

Fig. 2. Silicone rubber cast of the airways of the left lungs of *Micromys* (A), *Mus* (B), *Rattus* (C), and *Cricetomys* (D), view from ventral. Scale bar represents 10 mm.

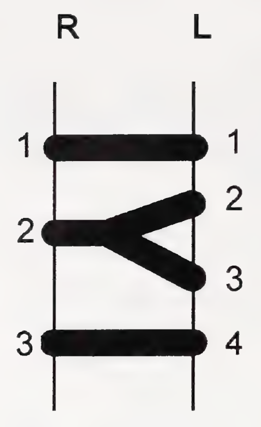


Fig. 3. Schematic drawing explaining the method of counting of the cartilage braces of the trachea. In this ventral view there are three free endings of braces on the right side and four free endings on the left side leading to an average of 3.5 braces in the illustrated part of the trachea.

For the purpose of this study three individuals each of *Micromys*, *Mus*, and *Cricetomys* and four *Rattus* were sacrificed, the lungs were stained and compared to lung casts of the same species.

All animals were killed by exposure to CO_2 and placed in a supine position. The trachea was opened and a cannula inserted. According to a method after SIMSON and VAN HORN (M. GÜNTERT, Bern, Switzerland, pers. comm.) the whole embryos were rendered translucent.

The lungs were excised from the thorax and filled with a solution containing 80 volume% 96% alcohol, 20 volume% glacial acetic acid and 30 mg Alcian blue. The lungs were fixed and stained for two days, being filled with and submerged in this solution. Then, the specimens were dehydrated in 99% alcohol for three to five days and macerated in a 1% KOH solution for another few days (until the lung becomes soft and lucent). In the last step, the specimens were immersed in a solution of 79 vol.% bi-distilled water, 20 vol.% glycerine and 1% KOH until they were completely translucent. The specimens could be stored in a solution of 50 vol.% 96% alcohol and 50% glycerin for long periods.

The translucent specimens were then analysed with the help of a stereo microscope and the dorsal endings of the cartilaginous braces were counted on the right and the left side and the average was calculated (Fig. 3). Further, the cartilaginous elements in the right and in the left lung were counted.

The length of the trachea was measured from the lower margin of the cricoid to the bifurcation into the main bronchi. The outer diameter of the trachea was taken in the middle of the distance between the cricoid and the bifurcation.

Results

In all species included in this study, only dorsally opened cartilaginous braces were found in the trachea and the main bronchi. Closed rings of cartilage encircling a bronchus could not be detected in any specimen. All four rodents showed the same distribution of chondroid braces over the identical parts of their conductive bronchial tree, regardless of the size of the lungs or the diameter of the bronchi. Figure 4 shows the stained translucent lungs of *Micromys*, *Mus*, *Rattus* and *Cricetomys*, all enlarged to the same size. For the original size relations of the lungs compare with figures 1 and 2.

Cartilage in the tracheal wall

These four rodent species possess dorsally open cartilaginous C-shaped braces in the trachea. The number of these chondroid elements differed among the species. *Micromys* and *Mus* showed 14 and 13 braces, respectively, the larger species *Rattus* and *Cricetomys* both had an average of 24 elements (Tab. 2). The bifurcation of the trachea into the two main bronchi was not supported by cartilage in the carina.

Cartilage in the bronchial walls

Both main bronchi possess cartilage up to the site of the first bifurcation. In the left lung, the cartilaginous braces of the main bronchus extend down to the point where the first ventral branch leaves the main bronchus, and 4–5 small cartilaginous elements can

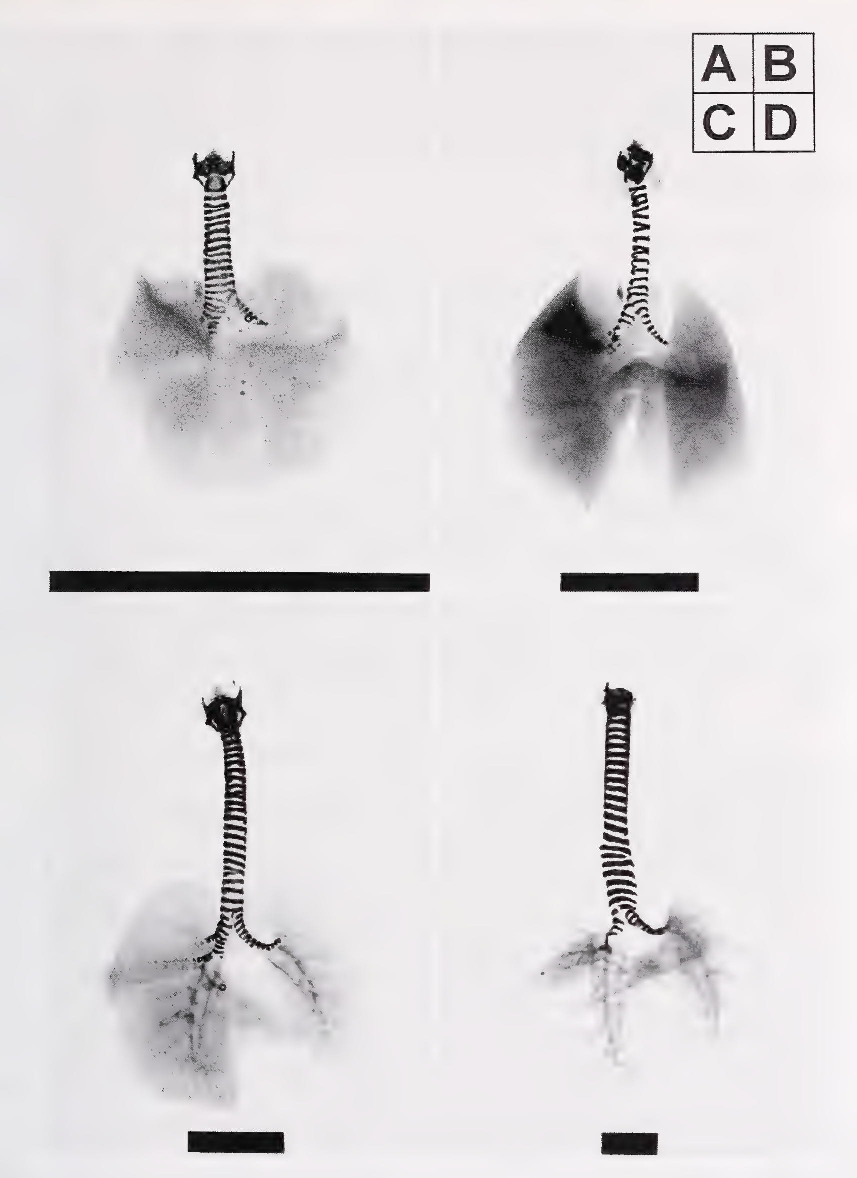


Fig. 4. Lungs of *Micromys* (A), *Mus* (B), *Rattus* (C), and *Cricetomys* (D). Translucent specimen showing the distribution and form of airway cartilage. All specimens are brought to identical size. Each scale bar represents 10 mm.

be found in this first ventral branch. In the right lung, the braces join the main bronchus down to the emerging bronchus of the middle lobe. Again, 3–4 cartilaginous elements can be found on this middle lobe bronchus (Tab. 3). In all specimens deserved, no cartilages could be detected in the carina. In the case of a bifurcation, the chondroid elements were placed in the wall opposite to the leaving branch, facing the carina (Fig. 5). Figure 4 shows the distribution of bronchial cartilage in the respiratory tracts of the four species.

Table 2. Diameter and length of trachea, in absolute terms and in % of nose-rump length, and number of cartilagineous braces in the trachea of *Micromys*, *Mus*, *Rattus*, and *Cricetomys*.

Species (n)	outer diameter of trachea	% of nose-rump length	length of trachea	% of nose-rump-length
Micromys (3)	2.0 mm	3.6%	6.8 mm	12.2%
Mus (3)	2.0 mm	2.0%	13.0 mm	12.7%
Rattus (4)	4.1 mm	1.9%	30.8 mm	14.6%
Cricetomys (3)	6.3 mm	1.8%	45.7 mm	12.8%

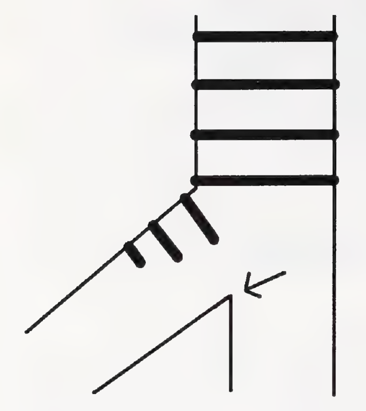


Fig. 5. Schematic drawing explaining the distribution of cartilage elements in a lobar bronchus exiting from the main bronchus. The arrow indicates the position of the carina. See also Fig. 4.

Table 3. Number of tracheal and bronchial cartilage braces in *Micromys*, *Mus*, *Rattus*, and *Cricetomys*.

Species (n)	braces in the left main bronchus	braces in right main bronchus	braces of trachea*
Micromys (4)	6.8	5.5	14.0
Mus (3)	8.0	5.0	13.7
Rattus (4)	8.5	9.5	24.0
Cricetomys (3)	8.4	6.0	24.0

* mean of left and right brace endings per trachea

Discussion

Functional aspects

The diameter of the airways and the stiffening of the airway walls by cartilaginous braces do not correspond, at least not when the trachea and the extrapulmonary bronchi are compared to the intrapulmonary bronchi, and when the intrapulmonary bronchi are compared to each other according to their positions and diameters.

All extrapulmonary airways in all four species are equiped with cartilage, regardless of their diameter. All intrapulmonary airways lack cartilage, at least, they possess no chondroid tissue soon after the bronchus enters the lung tissue.

Vanpeperstraete (1973) described principal differences in the form of intrapulmonary and extrapulmonary airway cartilage for several mammalian species (rat, dog, sheep, cow, pig, horse). He found regular braces in the trachea and main bronchi and described a sharp boundary to the irregular cartilage elements surrounding the intrapulmonary bronchi.

Extrapulmonary airways have regularly arranged, open C-shaped braces of cartilage. The dorsal part of the airways always remains free of cartilage, so that the airway is never completely surrounded by skeletal elements. The smooth airway musculature connects the open ends of the braces. For this reason, cartilage and muscles are arranged in the same layer of the airway wall.

Extrapulmonary airways in all mammals require cartilage stiffening in order to remain open under differing ambient pressures. The consequences of a pathological destabilisation of the tracheal cartilage elements in man reflects this function (Riede and Costabel 1993). A softening of the tracheal cartilage braces, tracheomalacia, results in a compression of the trachea known as "scabbard trachea" with a narrowing of its lumen.

Intrapulmonary airways in contrast show irregular elements, called plates. A single element is never closed around a bronchus in land-living mammals, but the plates cover the entire circumference of the bronchi. The musclature of these intrapulmonary bronchi in man lies between the epithelium and the cartilage as a closed layer, so that muscles and cartilage form two clearly separate layers of the bronchial wall (Duncker 1994). The cartilage elements in the intrapulmonary bronchial tree do not supply sites of fixation to the bronchial musculature.

These findings point to different functional parameters in extrapulmonary and intrapulmonary airway wall structure.

The intrapulmonary bronchial skeleton consisting of connective tissue and irregular cartilaginous plates is arranged external to the bronchial musculature, the latter determinig the diameter of the bronchi. These plates are not suitable for maintaining a patent bronchus because they do not regularly embrace more than half of the circumference of the bronchi.

The mechanism for maintaining intrapulmonary bronchi in an open condition in land-living mammals is the traction from the expanded lungs acting on these bronchi and the elastic retraction force of the respiratory lung tissue itself. The bronchial tree of mammals, apart from the function of distributing the oxygenated air as evenly as possible over the exchange surface, fulfills a second function, i. e., it is the main skeletal structure of the soft flexible lung tissue. It is hypothesized here, that when intrapulmonary airways in land-living mammals possess cartilage, as for example in man, it helps to prevent overexpansion of the bronchi and, additionally, acts as a fixation for the connective tissue, which stabilizes the inner structure of the lungs. As a consequence of this function, an instability of the intrapulmonary bronchial wall by distruction or aplasia of the cartilage plates leads to a widening of the bronchi, the condition known as bronchiectasis.

Nomenclature aspects

In the human anatomical nomenclature (Warwick and Brookes 1989), the terms "bronchus" and "bronchiolus" are defined by the presence or absence of cartilage, respectively, in the airway walls (Duncker 1994). According to this terminology obviously homologous parts of the bronchial tree of different animals have to be called "bronchi" in man and other larger mammals, but "bronchioli" in smaller species, simply because of the presence or absence of cartilage. For interspecific comparative investigations and descriptions of the mammalian lungs, a distinction between bronchi and bronchioli cannot be based on the criterion of cartilage in the wall. For example, in the myomorph rodents studied here, the principal airway of each lung should be called the main bronchiolus. The use of the diminutive for the largest intrapulmonary airways of an animal does not appear appropriate. On the other hand, in marine mammals the chondroid rigidity of the airways even includes the terminal bronchioles. In these marine forms cartilaginous spirals or closed rings occur (Belanger 1940; Denison et al. 1971; Engel 1956; Fiebiger 1915/16; Kooyman and Sinnett 1979; Wislocki 1929, 1942). They obviously keep the airways open against external water pressure.

The distinction between bronchi and bronchioli should be limited to human anatomy, where the term "bronchioli" has a long tradition. Neither the distribution of cartilage, nor the diameter, the epithelial lining, or the types of glands present, or any other morphological structure yields a basis for the definition of the term "bronchioli" that would be applicable to mammals of different body size or adapted to different environments. In consequence, the last generations of airway branches before opening into the acini should be called terminal bronchi and respiratory bronchi.

The term "cartilaginous ring" should be avoided as long as the element does not form a closed ring. To my knowledge, no such closed rings have ever been described in any trachea or bronchial tree of land-living mammals.

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Zusammenfassung

Größenunabhängige Verteilung von Bronchialknorpeln bei vier Arten myomorpher Nagetiere

Die Verteilung und die Form knorpeliger Stützelemente in der Wand der Luftwege von vier verschieden großen mäuseartigen Nagetieren wurden an Hand von knorpelgefärbten Aufhellungspräparaten dargestellt. Die Trachea und die extrapulmonalen Bronchen der euroasiatischen Zwergmaus, *Micromys minutus*, der Hausmaus, *Mus musculus*, der Wanderratte, *Rattus norvegicus* und der Gambia-Riesenhamsterratte, *Cricetomys gambianus*, weisen ausschließlich dorsal offene, regelmäßig angeordnete Knorpelspangen auf. Innerhalb des rechten Lungenflügels dehnt sich die Knorpelaussteifung mit wenigen Elementen bis auf den Abgang des Mittellappenbronchus vom Hauptbronchus aus, auf der linken Seite bis auf den ersten großen ventralen Bronchus, der den linken Hauptbronchus verläßt. Bei allen vier Arten setzt sich die Knorpelauskleidung bis zu einem identischen Punkt im Verzweigungsgefüge des Bronchialbaums fort und nicht bis zu einem bestimmten Durchmesser eines Bronchus. Aufgrund der sehr uneinheitlichen Knorpelverteilung in den Lungen der Säugetiere verschiedener Familien, Körpergrößen und Lebensweisen sollte der Begriff „Bronchiolus“ in der zoologischen und veterinärmedizinischen Terminologie nicht gebraucht werden. Es gibt keine Kriterien, die eine artübergreifend sinnvolle Definition des Terminus „Bronchiolus“ ermöglichen könnten. Nach der Funktion der Knorpelelemente in der Bronchialwand landlebender Säuger sollte unterschieden werden zwischen extrapulmonalen Knorpelspangen, die das Lumen der Luftwege offenhalten, und intrapulmonalen Knorpelelementen, die zur Stabilisierung der Bronchen gegen den sie weitenden Zug und als Ansatz für das die innere Lungenstruktur stabilisierende Bindegewebe dienen. Bei tauchenden Säugetieren dienen auch die intrapulmonalen Knorpelelemente der Offenhaltung der Bronchen.

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Diet of the Mountain vizcacha (*Lagidium viscacia* Molina, 1782) and food availability in northern Patagonia, Argentina

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Abstract

Diet of *Lagidium viscacia* and food availability were seasonally determined in La Payunia Protected Area through faecal analysis and point quadrat transects, respectively, in rocky elevations (shelter of mountain vizcachas) and adjacent plains. There were several evidences of selective feeding behaviour, besides the little similarity between diet and availability. The diet included only 33% of the plant genera occurring in the environment, the main dietary elements being three grasses (*Poa*, *Hordeum*, and *Stipa*) and one camephyte (*Acantholippia*). The proportion of grasses was significantly higher in the diet than in the environment, especially in the shrubby rocky elevations. The main food, *Poa*, was scarce to absent in rocky elevations, where *L. viscacia* lives, representing evidence of *L. viscacia*'s descending to plains for feeding. Similar behaviour was detected in *L. peruanum* and *Procavia johnstoni*, the rocky hyrax. The plains adjacent to rocky elevations in La Payunia were inhabited by the plains vizcacha, *Lagostomus maximus*, a closely related species to *L. viscacia*. Considerable similarity between both Chinchillidae diets suggests the possibility of competition, *Poa* being the key dietary element. Feeding behaviour of *L. viscacia* is focussed through the central place foraging theory, with rocky elevations as shelter against aerial predators.

Key words: Mountain vizcacha, Rodentia, feeding ecology, habitat use, plains vizcacha

Introduction

Mountain vizcachas (*Lagidium peruanum*, *L. viscacia*, and *L. wolffsohni*), chinchillas (*Chinchilla lanigera* and *C. brevicaudata*) and plains vizcacha (*Lagostomus maximus*) compose the family Chinchillidae (order Rodentia) (WOODS 1993). The mountain vizcacha is locally named "chinchillón" (Spanish for big chinchilla), due to its similarity to chinchillas (0.5 kg, MOHLIS 1983), but larger body size (1.5 kg, REDFORD and EISENBERG 1992). Of these three genera, *Lagidium* is the only one completely diurnal (PEARSON 1948).

All Chinchillidae are cave-dwelling and gregarious; "chinchillón" and chinchilla live in mountainous lands (ROWLANDS 1974; MANN 1978), while plains vizcacha uses grasslands and scrubby deserts exclusively (WEIR 1974; LLANOS and CRESPO 1952). *Lagidium* populations are present from 10° S (northern Peru) to 52° S (southern Chile and Argentina), in rocky environments of the Andean mountains and the Patagonian steppe (ROWLANDS 1974). Most populations – from 15° to 43° S – are currently attributed to *L. viscacia* (REDFORD and EISENBERG 1992). The natural fragmentation of the rocky habi-

tat makes a metapopulation structure presumable, that could increase its survival ability (WALKER et al. 1994).

Volcanic stone outcrops, where *L. viscacia* lives, characterize northern Patagonia. The irregular distribution of these outcrops is a determining factor of spatial differences in vegetation and soil (GONZÁLEZ DIAZ 1972; MÉNDEZ 1971). The special interest of this environment is that it is located within the narrow contact belt between the distributions of "chinchillón" (ROWLANDS 1974) and plains vizcacha (WEIR 1974).

The objectives of this study are to analyse the diet composition of *L. viscacia* in relation to food availability in a northern Patagonian environment, and to compare the diets of the two Chinchillidae species coexisting.

Material and methods

Study area and compared habitat characteristics

A study was conducted in La Payunia Reserve (Mendoza, Argentina, 36° 10′ S and 68° 50′ W, 2,500 km^2, elevation from 1,300 to 2,000 m). This area is located within the northernmost unit of the Patagonian Biogeographical Province (CABRERA and WILLINK 1980). The climate is of the continental desert type (CONSEJO FEDERAL DE INVERSIONES 1977). Mean seasonal temperature ranges from 6 °C in winter to 20 °C in summer, and annual precipitation averages 255 mm. The zone presents signs of strong past volcanic activity and of aeolian and hydric erosion. The resulting relief consists of gentle slopes and large plains, interrupted by basaltic steps and groups of hills (GONZÁLEZ DIAZ 1972). The xerophyllous vegetation, with a moderate mean cover (58%, PUIG et al. 1996), belongs to the Patagonic shrubby steppe. Almost all the shrubs are evergreen.

La Payunia was divided into habitats characterized by recurrent patterns of relief, soil, and vegetation, on the basis of 1 : 50,000 aerial photography, geological cartography (GONZÁLEZ DIAZ 1972) and plant cartography (MARTÍNEZ and DALMASSO 1993). Two different large habitats inhabited by "chinchillones" were selected: Huayquerías Coloradas (56 km^2) and Guadalosos (17 km^2). In both habitats we distinguished two microhabitats (plains and rocky elevations), in order to prove the exclusive use of rocky elevations by the "chinchillón". These elevations occupied 77 and 21%, respectively, of the mentioned habitat surfaces, and were constituted by outcrops of volcanic stone, and dominated by a shrubby stratum. Plains were characterized by a slightly rolling, sandy terrain, and a dominant herbaceous stratum.

Field and laboratory design

During 1991–1992 five samplings were carried out in two 10-ha zones, representative of the two habitats defined above. Samplings corresponded to winter (July), spring (October), summer (December and February), and autumn (May). Throughout the year, 32 faecal samples were collected and 18 to 29 transects were traversed in each sampling area to determine plant cover (as an estimator of food availability) by the point-quadrat method (DAGET and POISSONET 1971). Each sample, composed of 10 fresh pellets of "chinchillones", was collected from a different group of faeces. The 30-m transects were randomly distributed within each sampling area, separated from each other by more than 100 m. The number of transects was slightly higher in microhabitats with a more complex topography. Faecal samples were analysed through the microhistological method of BAUMGARTNER and MARTIN (1939), modified by DUCI (1949), using plant reference material from La Payunia stored in the Ruiz Leal Herbarium (IADIZA, Argentina). Genus level, and species level when possible, were reached.

Statistical analyses

Only the 19 plant species consumed by the "chinchillón" at least on one occasion (33% of those recorded in the two habitats) were considered. Plant species were grouped in four categories according to their life form: grasses, forbs, camephytes, and phanerophytes. Succulents were not foraged.

Availability and diet diversities were estimated using the Shannon-Wiener function (H′, COLWELL and FUTUYMA 1971). Kulczynski's coefficient (S_k, OOSTING 1956) was applied to estimate the similarities

between microhabitats. Significant differences in plant cover, diversity, and proportion of plant categories according to availability and diet among microhabitats were determined by the H statistic of Kruskall-Wallis ANOVA, and by the q statistic of the Tukey test for multiple comparisons (ZAR 1984).

The association between relative frequencies of species occurrence in diet and availability was analysed applying the Spearman's rank correlation coeffcient (r_s, SIEGEL 1986). Dietary preferences were detected by the IVLEV'S (1961) electivity index, and limits for the three ranks were fixed: (+0.3, +1.0) species eaten with preference (= species preferred), (–0.3, +0.3) species eaten with indifference, and (–1.0, –0.3) species eaten with avoidance (= species avoided). Dietary selectivity within each plant category was estimated using the index proposed by FEINSINGER et al. (1981).

Results

Food availabilities and use of microhabitats

Rocky elevations were the dominant relief in Huayquerías Coloradas, while plains dominated in Guadalosos. Rocky elevations appeared in groups of considerable extension in both habitats (73 and 14 ha average, respectively), and groups were separated from each other by a mean distance of 158 and 292 m, respectively. There was a mean distance of 33 m among rocky elevations, within each group. "Chinchillones" had sedentary habits, and were usually observed sunbathing on the rocks. No "chinchillón" was ever observed in the wide plains.

Table 1. Mean composition of *L. viscacia* diet, average availability of consumed species in each type of microhabitat, and IVLEV'S (1961) electivity index calculated with the availability in rocky elevations.

	Consumed plant species	Availability in:		Diet of *L. viscacia*	Electivity in rocky elevations
		rocky elevations	plains		
Ho	*Hordeum* spp.	0.0010	0.0006	0.1871	0.9899
Br	*Bromus* spp.	0.0009	0.0007	0.0174	0.9042
Po	*Poa* spp.	0.0113	0.0804	0.4244	0.9480
St	*Stipa* spp.	0.5300	0.2074	0.1366	–0.5902
Sp	*Sporobolus rigens*	0.0923	0.4323	0.0400	–0.3955
Pa	*Panicum urvilleanum*	0.0610	0.2732	0.0420	–0.1844
Ar	*Aristida* spp.	0.0006	0.0003	0.0314	0.9616
Se	*Setaria mendocina*	0.0007	0.0004	0.0074	0.8342
Di	*Digitaria californica*	0.0007	0.0004	0.0076	0.8285
	GRASSES TOTAL	0.6985	0.9958	0.8938	
Dr	*Draba* spp.	0.0001	0.0001	0.0005	0.5352
Le	*Lesquerella mendocina*	0.0003	0.0002	0.0050	0.8933
Ni	*Nicotiana spegazzini*	0.0002	0.0001	0.0020	0.8127
	FORBS TOTAL	0.0006	0.0004	0.0075	
Ve	*Verbena* spp.	0.0781	0.0033	0.0120	–0.7334
Ac	*Acantholippia seriphioides*	0.1431	0.0000	0.0771	–0.2998
At	*Atriplex lampa*	0.0003	0.0002	0.0024	0.7898
	CAMEPHYTES TOTAL	0.2216	0.0035	0.0915	
Ep	*Ephedra ochreata*	0.0771	0.0000	0.0026	–0.9348
Ly	*Lycium chilense*	0.0016	0.0003	0.0030	0.2987
Pr	*Prosopis* spp.	0.0002	0.0000	0.0002	–0.0508
Be	*Berberis grevilleana*	0.0004	0.0000	0.0014	0.5523
	PHANEROPHYTES TOTAL	0.0794	0.0003	0.0072	

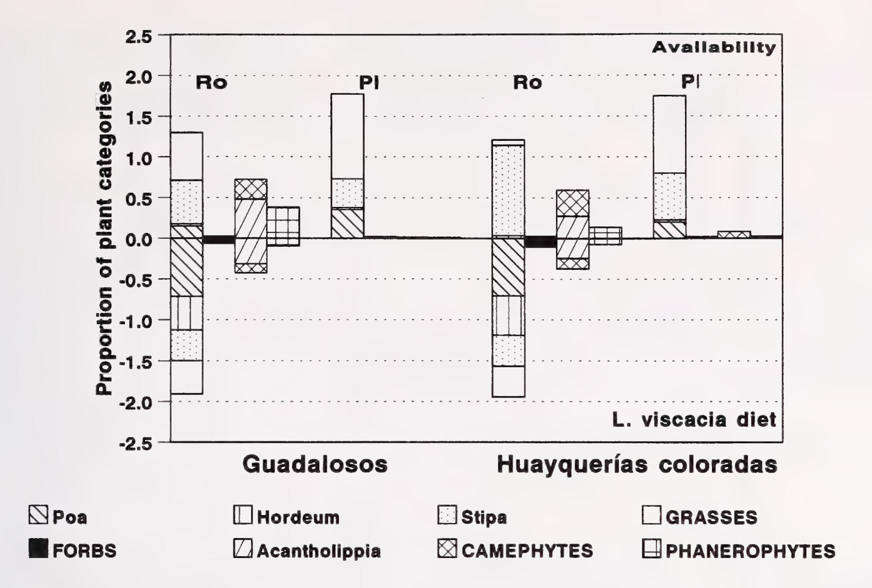


Fig. 1. Annual mean proportion of plant categories in food availability (upper half of the graph) and in *L. viscacia* diet (lower half) in each habitat. The availability in the two types of microhabitats (Pl: plains and Ro: rocky elevations) is considered separately. Different fillings allow to recognize the four main dietary species within their respective categories. Relative frequencies were transformed using the arc-sin-square root to make differences between availability and diet more visible, especially for scarce categories.

Within the 19 plant species consumed by "chinchillón", the most available on rocky elevations were the grass *Stipa* and the camephyte *Acantholippia* (Tab. 1), which were representative of herbaceous and low shrubby strata, respectively (Fig. 1). The herbaceous stratum reached 99% of plant availability in adjacent plains, where availability of the grasses *Sporobolus* and *Panicum* surpassed that of *Stipa*, while *Acantholippia* was absent. The grass *Poa* was present in the plains but not in rocky elevations of Huayquerías Coloradas; in Guadalosos the proportion of *Poa* was higher in plains than in rocky elevations ($H = 46.6$ $p = 4.0$ e^{-10}). Forbs availability was very scarce in all microhabitats (<0.1%), and higher values were obtained ($H = 69.0$ $p = 3.7$ e^{-14}) during summer and autumn (Fig. 2).

Plant cover in rocky elevations was significantly lower ($H = 41.9$ $p = 4.2$ e^{-9}) than in the adjacent plains (Tab. 2). Rocky elevations also differed from plains due to lower availability of grasses ($H = 52.4$ $p = 2.5$ e^{-11}) and higher availability of camephytes ($H = 40.6$ $p = 8.1$ e^{-9}). High relative abundance of *Stipa* in Huayquerías Coloradas rocky elevations (80%) determined a significantly lower diversity than in the other microhabitats ($H = 34.8$ $p = 1.4$ e^{-7}), and a moderate similarity with Guadalosos rocky elevations ($S_K = 0.41$). Huayquerias Coloradas rocky elevations significantly differed from those of Guadalosos, due to higher availability in the former of forbs ($H = 9.5$ $p = 0.024$) and grasses (particularly *Stipa* ($H = 49.2$ $p = 1.4$ e^{-10}) and *Hordeum* ($H = 8.7$ $p = 0.03$)), and lower availability of the camephyte *Acantholippia* ($H = 44.6$ $p = 1.1$ e^{-9}) and phanerophytes ($H = 41.9$ $p = 4.1$ e^{-9}).

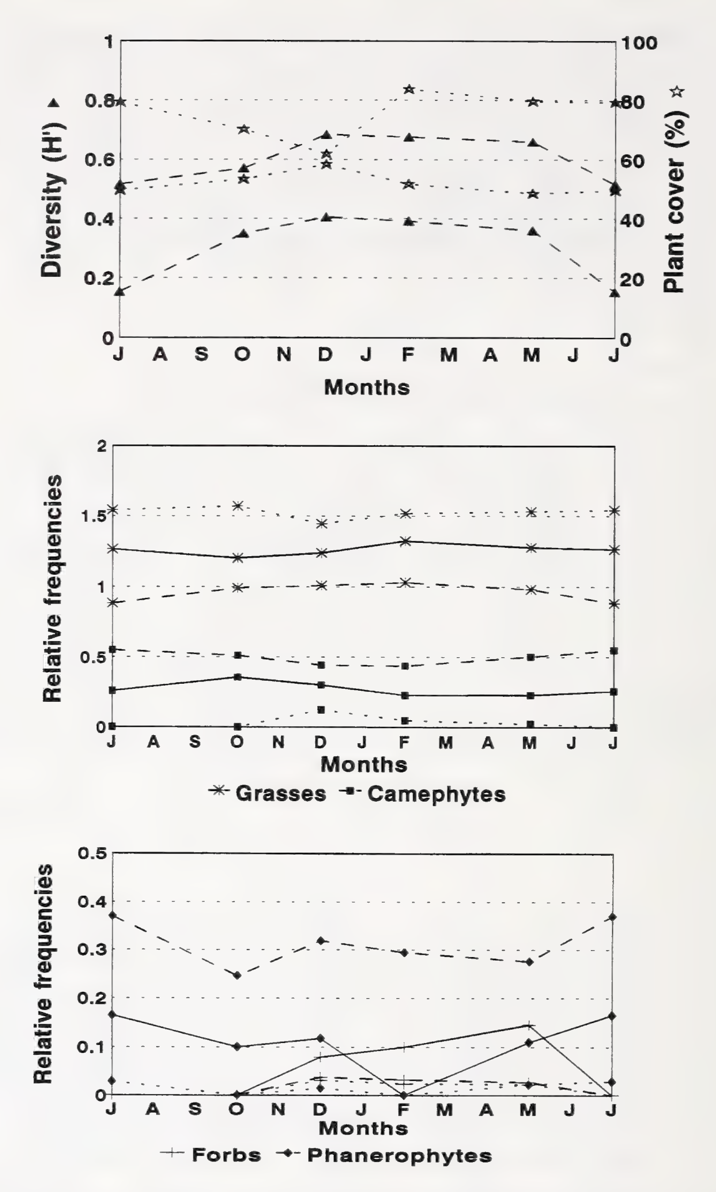


Fig. 2. Seasonal values of plant cover, diversity, and proportion of plant categories in the diet of *L. viscacia* (solid line) and in food availability in rocky elevations (dashed line) and plains (dotted line).

Diet of the "chinchillón"

Despite the dominance of shrubby species in rocky microhabitats, 9 of the 19 consumed genera were grasses (Tab. 1). These comprised most of the diet (89%), followed by camephytes (9%) (Fig. 1). Food niche breadth was high (Tab. 2) in spite of the low dietary richness.

The grasses *Poa*, *Hordeum*, and *Stipa*, and the camephyte *Acantholippia* were considered main elements in the diet of "chinchillón", taking into account their frequent use

(dietary proportions higher than 5%) throughout the year. The rest of the grasses and the camephyte *Verbena* showed dietary proportions between 1 and 5%, and were classified as complementary elements. Forbs proportions increased in summer and autumn in the diet (H = 14.04 p = 0.019), as well as in availability (Fig. 2), and constituted seasonal dietary elements.

The use of *Stipa* was higher in early summer than in autumn (H = 18.70 p = 0.001), and the contrary occurred with *Poa* (H = 10.97 p = 0.027), without seasonal changes detected in their respective availabilities.

The similarity between diets obtained in Huayquerías Coloradas and in Guadalosos was very high (S_K = 0.91). Nevertheless, and according to differences in availability, a lower food niche breadth was obtained in Huayquerías Coloradas than in Guadalosos (H = 4.88 p = 0.022), with a higher proportion of grasses (H = 3.91 p = 0.048), particularly *Hordeum* (H = 7.96 p = 0.004), and a lower proportion of camephytes (H = 6.86 p = 0.009), particularly *Acantholippia* (H = 9.60 p = 0.002), in the former.

In spite of being present only in the plains, *Poa*, *Panicum*, and *Sporobolus* were included in the diet of "chinchillón" in Huayquerías Coloradas.

Dietary preferences

Similarity between diet and availability was moderate to low (Tab. 2), with significant associations for all the analysed cases, except for Huayquerías Coloradas rocky elevations. Diet was closer to rocky elevations plant availability in Guadalosos, but closer to plains availability in Huayquerías Coloradas. No significant difference was detected between diet and availability in Guadalosos rocky elevations, except for the forbs category. In both Huayquerías Coloradas microhabitats, differences were detected for grasses and camephytes, the most frequently consumed categories. The use of the main species – as a set – differed from the availability in all microhabitats.

The "chinchillón" preferred 67% of the grasses, the three forbs, the camephyte *Atriplex* and the phanerophyte *Berberis* (Tab. 1). Most of the preferred genera presented low proportions in the diet, except for the grasses *Poa*, *Hordeum*, *Aristida*, and *Bromus*. The camephyte *Acantholippia* and the grass *Panicum* were used with indifference, as well as the phanerophytes *Lycium* and *Prosopis* which presented low proportions. The coarse grasses *Stipa* and *Sporobolus*, the camephyte *Verbena* and the phanerophyte *Ephedra* were used with avoidance.

Selectivity within the available grasses was higher, but lower within camephytes, in Guadalosos rocky elevations than in the other microhabitats. Selectivity within the four frequently used species was highest in Huayquerías Coloradas rocky elevations (Tab. 2).

Comparison between *Lagidium viscacia* and *Lagostomus maximus* diets

Plains in both analysed habitats were occupied by plains vizcacha, whose diet was composed of 23 plant species in Huayquerías Coloradas and 21 species in Guadalosos, and dominated by grasses (95 and 97%, respectively) (Puig et al. 1997).

There was considerable similarity between "chinchillón" and plains vizcacha diets in Guadalosos as well as in Huayquerías Coloradas (0.70 and 0.68, respectively). Both Chinchillidae preferred the grass *Poa*, which was their major food (Fig. 3). In both cases *Stipa* was also intensively used, although with avoidance. There were no differences between "chinchillón" and plains vizcacha diets in the proportions of *Poa* (Z = 1.23 p = 0.221), *Aristida* (Z = 1.64 p = 0.100), *Nicotiana* (Z = 0.77 p = 0.445), and *Verbena* (Z = 1.59 p = 0.112).

The most important differences between "chinchillón" and plains vizcacha diets were due to a higher use of the camephyte *Acantholippia* (Z = 7.43 p = $1.1\ e^{-13}$), and a lower use of the grass *Panicum* (Z = 9.41 p = $1.0\ e^{-20}$) by the former.

Table 2. *L. viscacia* diet and food availability in Huayquerías Coloradas (HC) and Guadalosos (GU) segregating plains (pl) and rocky elevations (ro). Levels of significance in tests (p) appear in brackets. The group of main species (*Hordeum*, *Poa*, *Stipa* and *Acantholippia*) is analysed separately (Ho-Po-St-Ac).

	HC ro	HC pl	GU ro	GU pl
	Availability of consumed species			
Plant cover	25.80	75.86	40.53	74.01
Diversity	0.317	0.474	0.783	0.541
	Diet of *L. viscacia*			
Food niche breadth	0.779		0.786	
	Comparison between diet and availability			
Similarity	0.220	0.252	0.373	0.343
Association	0.137	0.708	0.704	0.541
	(0.562)	(0.003)	(0.003)	(0.022)
	Differences per category according to Mann-Whitney test			
Grasses	4.63	2.81	1.97	6.37
	($4\ e^{-6}$)	(0.005)	(0.049)	($2\ e^{-10}$)
Forbs	1.61	1.24	3.02	3.20
	(0.106)	(0.214)	(0.003)	(0.001)
Camephytes	4.37	2.21	1.20	6.16
	($1\ e^{-5}$)	(0.027)	(0.231)	($8\ e^{-10}$)
Fanerophytes	1.41	0.05	1.99	2.75
	(0.160)	(0.957)	(0.046)	(0.006)
Ho-Po-St-Ac	6.19	2.18	2.84	2.44
	($6\ e^{-10}$)	(0.030)	(0.005)	(0.015)
	Selectivity of plant categories by *L. viscacia*			
Grasses	0.392	0.401	0.605	0.482
Forbs	0.952	0.992	0.975	0.993
Camephytes	0.984	0.969	0.873	0.949
Fanerophytes	0.999	0.998	0.998	0.998
Ho-Po-St-Ac	0.643	0.641	0.865	0.861

Discussion

Several pieces of evidence suggest that "chinchillón" developed a selective feeding behaviour in La Payunia: it uses only 33% of the available plant genera; similarity between diets is higher than similarity between the respective availabilities; grass category comprises a significantly higher dietary proportion than that available in rocky elevations.

L. viscacia in a Subantarctic forest (Neuquén, Argentina, Galende 1995) also showed a considerable proportion of grasses (68%) in the diet, despite the lesser importance of the herbaceous stratum. Two of the three most frequently consumed grasses in Neuquén (*Stipa* and *Poa*) coincide with the most commonly eaten ones in La Payunia. Another grass, *Festuca orthophylla*, was found to be *L. viscacia*'s main food in northern Chile, in places where coarse grasslands surrounded rocky elevations, but the Juncaceae *Oxychloe andina* and *Distichia muscoides* were the most frequently eaten species when "bofedales" (high Andean moist lands) were accessible (Palma 1985). *L. peruanum* diet in Perú (Dávila et al. 1982) differed from that of *L. viscacia* due to the inclusion of Cactaceae by the former.

The considerable dietary proportion and scarce availability of *Hordeum*, a grass with high nutritional value (Dalmasso pers. comm.), suggest that the "chinchillón" developed a remarkable search behaviour for its food.

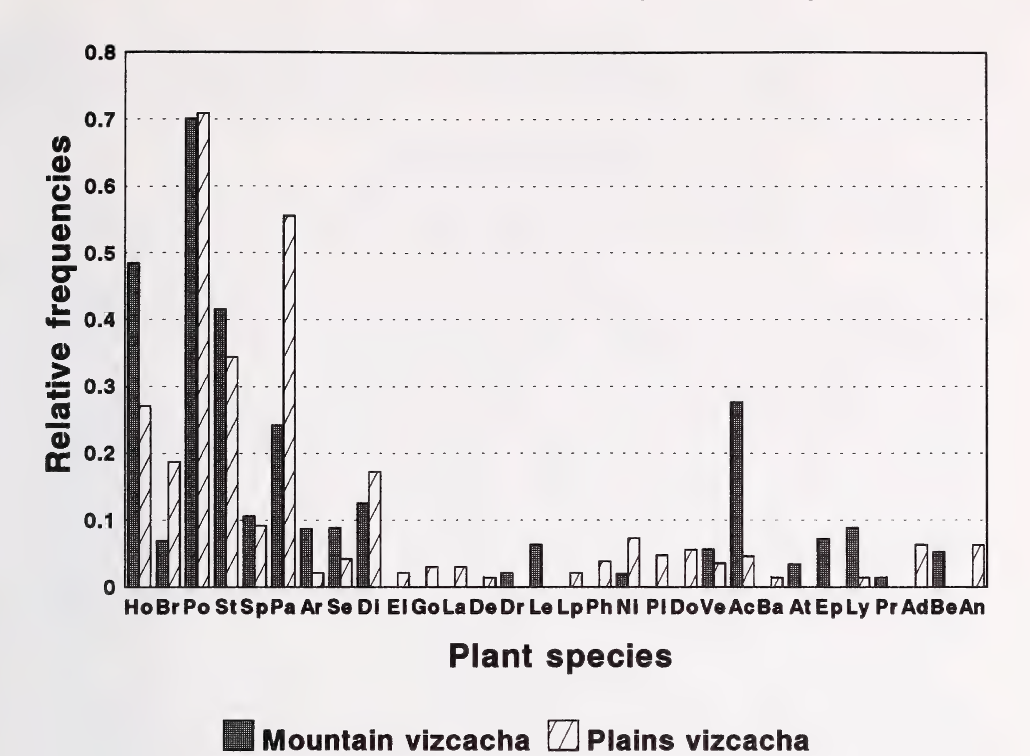


Fig. 3. Annual mean proportion of plant species eaten by *Lagidium viscacia* (identified in Tab. 1) or by *Lagostomus maximus* (El: *Elymus eranthus*, Go: *Gomphrena* sp., La: *Lappula redowsky*, Ph: *Phacelia artemisioides*, Pl: *Plantago patagonica*, Do: *Doniophyton* sp., Ba: *Baccharis darwini*, Ad: *Adesmia* spp., and An: *Anarthrophyllum rigidum*). Relative frequencies were transformed using the arcsin-square root.

"Chinchillón" uses with avoidance only those grasses characterized by roughness (*Stipa* and *Sporobolus*, Wainstein and González 1962). In fact, dietary selectivity within grasses is higher where *Stipa* comprises almost all the availability of this category. The avoidance is only attenuated in early summer, when these grasses have buds. *Stipa* relevance and *Sporobolus* presence in the diet could be explained by the fact that these genera are the most available in rocky elevations and plains, respectively. A similar behaviour was observed in other herbivores coexisting with "chinchillón" in La Payunia, such as plains vizcacha (Puig et al. 1997) and guanaco (*Lama guanicoe*) (Puig et al. 1996).

The low quality of *Acantholippia* (Dalmasso pers. comm.) does not agree with its importance in the diet, taking into account that it was the only shrub included among the main dietary elements. The high use of this camephyte could be a consequence of its high availability in rocky elevations.

The predominance of grasses in "chinchillón" diet, taking into account the number of species as well as their proportions, is emphasized by the importance of the shrubby stratum in rocky elevations where the "chinchillón" lives. Moreover, the main dietary element (*Poa*) is eaten with preference throughout the year, despite its low availability in Guadalosos rocky elevations, and its null availability in those of Huayquerías Coloradas. The latter case can be considered as evidence of "chinchillón" reaching this grass by descending to plains, where the herbaceous stratum had a higher availability. A similar

behaviour has also been observed by Hoeck (1975) in the hyrax *Procavia johnstoni* (Hyracoidea, Procaviidae) in Serengeti (Tanzania); this hyrax lives in rocky elevations, it has a strong preference for grasses and has to go outside the elevations for grazing. *Lagidium peruanum* of Caccachara (Perú) descends to feed as far as 70 m away from rock slides, to cirques with abundant vegetation (Pearson 1948).

The plains vizcacha lives in the wide plains of La Payunia where it builds large burrow systems, around which a loss of the plant cover occurs due to its feeding activity (Puig et al. 1997). Several dietary differences reflect the availability of their respective microhabitats, such as a higher proportion of *Panicum* (the most abundant grass in the plains) in plains vizcacha diet, and a higher proportion of *Acantholippia* (a camephyte characteristic of rocky elevations) in "chinchillón" diet. Nevertheless, there is considerable similarity between "chinchillón" and plains vizcacha diets.

Plains vizcachas do not visit rocky elevations (Puig et al. 1997) but "chinchillones" may graze in the plains close to the elevations; therefore, spatial segregation between these rodents does not seem to be complete. These two microhabitats present frequent contact surfaces in La Payunia, alternating in a mosaic-like design. Encounters between "chinchillón" (diurnal) and plains vizcacha (nocturnal) are not likely to occur, since their activity patterns differ. This would prevent any development of the behavioural mechanisms needed for spatial segregation.

Poa, occurring almost exclusively in plains, may be considered a key element in the diet. Potential competition for *Poa* between plains vizcachas and "chinchillones" needs to be evaluated, taking into account its limited availability in La Payunia.

Rocky elevations and dense high vegetation were indicated as suitable shelters for rodents whose key predators were aerial (Lima and Dill 1990). On the other hand, patches with low plant cover and good visibility were selected by rodents (Cassini 1991) and passerines (Lima et al. 1985) whose main predators were terrestrial. Both types of predators exist in La Payunia, and mountain lion (*Puma concolor*) has been identified as an important predator of plains vizcachas (Branch et al. 1994; Puig et al. 1997). "Chinchillón", with a lower body weight than plains vizcacha, might have mainly aerial predators, relying in the former anti-predator defence alternative. The rock hyrax *Procavia capensis*, whose habitat seems similar to that of "chinchillón", is one of black eagle's (*Aquila verreauxii*) main preys in Zimbabwe (Barry 1996). Pearson (1948) observed the Canidae culpeo (*Pseudalopex culpaeus*) pursuing mountain vizcachas among the rocks in Caccachara (Perú), but considered it a surprisingly unsuccessful predator of *L. viscacia*. Also Palma (1985) observed culpeos trying to prey on mountain vizcachas without success in northern Chile, and he considered the raptor gurney's buzzard (*Buteo poecilochrous*) a predator of *L. viscacia*. The diurnal Accipitridae black chested buzzard eagle (*Geranoaetus melanoleucus*) and red backer buzzard (*Buteo polyosoma*) were frequently observed in La Payunia, and may prey upon "chinchillones". Nevertheless, we have no evidence of "chinchillón" predation by canids or raptors.

If predation is mainly aerial, the visits to herbaceous plains would represent a considerable risk for the "chinchillón", suggesting a great importance of grasses, particularly *Poa*, in the diet. An increase in dietary selectivity according to distance from rocky elevations, as predicted by the central place foraging theory (Andersson 1981), has been described for North American pikas (*Ochotona princeps*, Lagomorpha, Ochotonidae) by Huntly et al. (1985). This could also be the case for "chinchillón".

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Zusammenfassung

Nahrung des Bergvizcacha (Lagidium viscacia Molina, 1782) und Nahrungsquellen in Nordpatagonien, Argentinien

Nahrungszusammensetzung und Nahrungsquellen des Bergvizcacha im Naturschutzgebiet La Payunia wurden jahreszeitlich untersucht durch Exkrement- und Habitatanalysen in den felsigen Höhengebieten (Zufluchtsort der Bergvizcachas) und angrenzenden Ebenen: Es bestand ein geringer Zusammenhang zwischen Ernährung und Vielfalt der Nahrungsquellen. Nur 33% der vorkommenden Pflanzenarten wurden gewählt, hauptsächlich die drei Gräser *Poa*, *Hordeum* und *Stipa*, sowie die Chamephyte *Acantholippia*. Der Anteil aufgenommener Gräser war deutlich größer als deren Vorkommen in den öden Felsgebieten. *Poa*, die Hauptnahrung, kam spärlich vor oder fehlte in den felsigen Wohngebieten von *Lagidium viscacia.* Dieses läßt vermuten, daß die Tiere zur Nahrungsaufnahme in die Täler hinabsteigen. Ähnliches Verhalten wurde bei *Lagidium peruanum* und auch bei *Procavia johnstoni* festgestellt. Die, den Felsregionen vorgelagerten Ebenen werden von den Talvizcachas (*Lagostomus maximus*) bewohnt, einer den Bergvizcacha nahe verwandten Art. Die grundsätzlich ähnliche Ernährung dieser beiden Arten läßt ein Wettbewerbsverhalten vermuten. Für beide ist *Poa* Grundnahrungsmittel. Die felsigen Höhengebiete dienen der körperkleineren Art wahrscheinlich als Zufluchtsort vor Predatoren aus der Luft.

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A survey of large mammals in the central Annamite mountains of Laos

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Abstract

Large mammals were surveyed using direct observation in montane Laos during April–May 1996 in little-disturbed evergreen forest in and around the Nakay-Nam Theun National Biodiversity Conservation Area (NBCA). Survey focussed on one road, where low hunting pressure and excellent viewing conditions gave the truest representation of relative species status at any Lao site yet surveyed. More large mammal species have been found there than in some entire NBCAs; the total of 15 species of carnivore is especially noteworthy. Nocturnal contact rates (if lorises are excluded from the comparison) were the highest of any Lao site yet surveyed. Encounter rates by day were also high. Totals of nine Globally Threatened, three Data Deficient and six Nationally At Risk species are of outstanding conservation importance. Many have large populations and some have not otherwise been seen in the field on a recent survey programme in Laos. A few additional species were found on another road where survey conditions were less good. Results from the area, compared with those from lowlands and foothills in southern Laos, suggest the following altitudinal distributions: (1) sympatric species in the genera *Petaurista*, *Rhizomys*, and *Manis* are separated altitudinally; (2) *Arctonyx collaris*, *Paguma larvata*, and *Herpestes urva* are submontane or montane; (3) *Nycticebus coucang* is commoner in the lowlands than at 1 000 m.

Key words: Laos, mammalian species, altitudinal zonation

Introduction

The Annamite mountains along the border of Laos with Viet Nam are a centre of mammalian endemism. However, prior to 1996, no direct field observations of nocturnal large mammals (those identifiable without capture) had been made in Laos above 550 m altitude. Historically, very little work on mammals took place in Laos, and much of this consists of anecdotal writings by hunters (summarised in Deuve 1972 and citations therein). The political situation prevented any new work from 1972 until 1989. Mammal surveys by night in Laos since then were in the lowlands and foothills and direct searching by day was also limited (Salter 1993; WCS unpubl. data, summarised in Duckworth 1997). Work in the Annamites targetted certain species and used mainly trophy examination, village interviews and signs: *Pseudoryx nghetinhensis* Dung, Giao, Chinh, Tuoc, Arctander and Mackinnon, 1993 (Saola) (Schaller and Rabinowitz 1995); *Megamuntiacus vuquangensis* Tuoc, Dung, Dawson, Arctander and MacKinnon, 1994 (Giant Muntjac) (Schaller and Vrba 1996; Timmins et al. 1998); *Sus bucculentus* Heude, 1892 (Vietnamese Warty Pig) (Groves et al. 1997) and an undetermined muntjac *Muntiacus* sp. (Timmins et al. 1998). During recent surveys throughout Laos (sites summarised in Duckworth 1997), large mammals were problematical to record: they are shy (due to widespread hunting) and many species are nocturnal, yet identification from indirect evidence (signs and vil-

lage information) is difficult as most groups contain several similar species. Few modern publications cover a wide range of large mammal species in Laos: DUCKWORTH et al. (1994), BERGMANS (1995), RUGGERI and TIMMINS (1996), and DUCKWORTH (1996, 1997).

The Nakay-Nam Theun National Biodiversity Conservation Area (NBCA) and the Nam Theun Extension occupy a large area in the Annamites. A survey in 1994 concentrated on mammal signs and birds (EVANS and TIMMINS 1998; WCS unpubl. data). To expand on this, large mammals were surveyed by direct observation in both areas during April–May 1996. Problems with permission curtailed work in Nam Theun Extension and heavy rain reduced the ability to observe mammals while there.

This study compares the two communities with other sites in Laos, using mainly the large amount information published as internal reports to the Lao government by the Wildlife Conservation Society (WCS). Statements summarising recent records consider fieldwork until October 1996 (largely summarised in DUCKWORTH 1997).

Material and methods

Study area

The Nakay-Nam Theun NBCA (17°34′–18°23′ N 105°02–46′ E) is, at 3 445 km², the largest protected area in Laos. It is mostly within the Annamite mountains. At the heart, 800 km² of mountains rise mostly above 1 000 m, with the summit ridge (forming the international border) exceeding 2 200 m. Route 8 crosses from Laos to Viet Nam and constitutes the northern border of the NBCA. North of

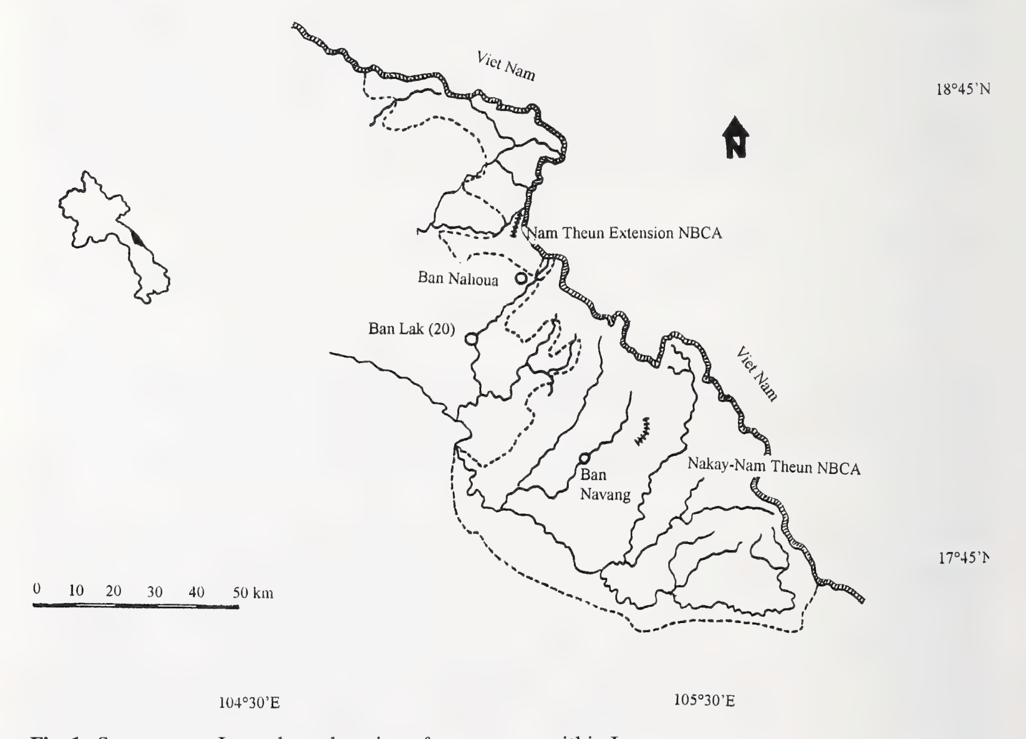


Fig. 1. Survey area. Inset shows location of survey area within Laos.
Only major rivers are shown. Ban Lak (20) is the only major town in the area of the figure. Small villages not referred to in the text are not shown.
++++ survey road; ~ river; - - - boundary of protected area; ┬┬┬ international boundary

this road, approximately 550 km^2 of forested Annamites (at 18°20-45′N 104°56′-105°12′E) form the proposed Nam Theun Extension. The area is shown in figure 1. Both NBCAs contain extensive little-degraded evergreen forest. The low Annamite spine in the Nam Theun Extension (mostly 600–900 m) allows winds from both east and west and so rain falls in most months; in contrast, most of Nakay-Nam Theun has a dry season in November–April. Recently constructed roads run from the border through little-degraded forest into each area. These roads allow more frequent sighting of mammals than in unbroken forest, so all observation was conducted from roads.

Nakay-Nam Theun NBCA at 17°57–18°03′ N 105°18–26′ E; 24 April–14 May 1996

A road from the village of Ban Navang into Nakay-Nam Theun was aimed towards the headwaters of the Nam Xot. Construction occurred intermittantly from late 1993 to March 1995, when the road extended about 18.5 km east of Ban Navang (R. J. Timmins verbally 1994–1996). The road has not been used for its intended purpose, to transport the extremely valuable *Fokienia* logs. The road traversed primary montane seasonally dry evergreen forest. No people lived along it and hunting pressure was low; occasional rattan collecting trips, using a lorry, kept the road open. Two patches were surveyed: the extensive block from the road tip back west for about 5 km (1 000–1 300 m altitude), and, west of this, a large patch at 700–900 m; forest links these away from the road.

Nam Theun Extension NBCA at 18°25–30′ N 105°04–07′ E; 13–22 April 1996

Construction for six months to April 1996 extended a road 28 km from Ban Nahoua; the last 9 km ran through little-disturbed wet evergreen forest. Several dozen labourers camped in the middle of the survey area and some hunting probably occurred. The road was still under construction and about a dozen vehicles passed daily. The eastern extent, at 1 000–1 300 m altitude, passed through wet evergreen forest containing many *Fokienia* trees (then being felled), but to the west these trees were absent; most of this area was at 800–1 000 m, with an isolated summit of 1 250 m.

The Nam Theun Extension road ran along steep hills and heavy traffic has incised it deeply, so that for much of its length ground-living mammals must negotiate 1–4 m slopes of unfixed soil to reach the road. Most of the Nakay-Nam Theun road is level with adjacent land and thus, irrespective of the actual mammal communities, ground-living mammals would be more likely to use it than the Nam Theun Extension road. The relatively low and broken canopy was observed easily from both roads.

Observations

Nocturnal mammals were counted while walking equipped with a headtorch and high power spotlamp, following the methodology of Duckworth et al. (1994). Work was not performed under a bright moon in case encounter rates were reduced. Results are presented as the number of observations related to search time, with no attempt to calculate population densities.

Extensive diurnal observations were made along the road in Nakay-Nam Theun. The observer spent periods of 1–5 hours sitting inconspicuously at points with a clear view of a long stretch of road or, in one case, down a landslip. When rain had dampened the leaf litter, the observer walked silently along the road. Few diurnal observations were made in Nam Theun Extension as time was short.

Notable observations from other biologists visiting during 1994–1996 are presented. Their records are asterisked (*) in the text as, to allow comparison of the main survey with future work, diurnal survey effort (number of days in the field) must be clear. Other people's time should not be included in this as they were not primarily searching directly for mammals.

Results

Taxonomic limits, scientific nomenclature and systematic sequence follow Reeder and Wilson (1993). Key species of mammals refer to those Globally Threatened, Globally Near-Threatened, and Data Deficient, following IUCN (1996), or Nationally at risk, following Salter (1993).

Table 1. Mammal species recorded along the two roads

Species	Threat	NNT road		NTX road	
		1996	1994	1996	1994
Tupaia belangeri (Wagner, 1841); Northern treeshrew		F	P	F	C
Nycticebus coucang (Boddaert, 1785); Slow loris	NAR	O	P	O	
[*Nycticebus pygmaeus* Bonhote, 1907; Pygmy loris]	GT	[O]		[O]	
Macaca arctoides I. Geoffroy, 1831; Stump-tailed macaque	GT	O	P		Pd
Macaca assamensis M'Clelland, 1840; Assamese macaque	GT	F	[P]		
Pygathrix nemaeus (Linnaeus, 1771); Douc langur	GT	C	P		[Pr]
[*Trachypithecus phayrei* (Blyth, 1847); Phayre's langur]	DD	[O]			
Hylobates leucogenys Ogilby, 1840/*H. gabriellae* Thomas, 1909; Gibbon	DD	C	C	C	O
Prionailurus bengalensis (Kerr, 1792); Leopard cat	NAR	P	[Ps]		
Neofelis nebulosa (Griffith, 1821); Clouded leopard	GT	P			
Panthera pardus (Linnaeus, 1758); Leopard	NAR	P			
Panthera tigris (Linnaeus, 1758); Tiger	GT	P	Ps		[Pr]
Pardofelis marmorata (Martin, 1837); Marbled cat	DD	P			
Herpestes urva (Hodgson, 1836); Crab-eating mongoose		P			
Arctonyx collaris F. G. Cuvier, 1825; Hog badger		P		P	
Martes flavigula (Boddaert, 1785); Yellow-throated marten		F	P	P	P
Mustela sibirica Pallas, 1773; Siberian weasel		P			
Mustela strigidorsa Gray, 1855; Back-striped weasel	GT		P		
Arctogalidia trivirgata (Gray, 1832); Small-toothed palm civet		C	P		
Paguma larvata (Smith, 1827); Masked palm civet		O		P	
Paradoxurus hermaphroditus (Pallas, 1777); Common palm civet		C	P	F	P
Prionodon pardicolor (Hodgson, 1842); Spotted linsang	NAR	P	P		
Viverra zibetha Linnaeus, 1758; Large Indian civet		F			
Sus sp(p).; Pig		P	Ps		Ps
Tragulus javanicus (Osbeck, 1765); Lesser mousedeer					[Ps]
Cervus unicolor Kerr, 1792; Sambar			[Ps]		
Muntiacus muntjak (Zimmermann, 1780); Indian muntjac		P	Pdv		P
Megamuntiacus vuquangensis Tuoc et al., 1994; Giant muntjac	n/a	[P]	[P]		Pdv
Muntiacus/Megamuntiacus spp.		C	C	O	P
Bos frontalis Lambert, 1804; Gaur	GT	P	[Ps]		
Manis pentadactyla Linnaeus, 1758; Chinese pangolin	GNT			P	
Callosciurus erythraeus (Pallas, 1778); Pallas's squirrel		C	C	C	C
Callosciurus inornatus (Gray, 1867); Inornate squirrel	GT		P	P	
Ratufa bicolor (Sparrman, 1778); Black giant squirrel	NAR	C	P	P	P
Dremomys rufigenis (Blanford, 1878); Red-cheeked squirrel		C	C	C	C
[*Tamiops maritimus* (Bonhote, 1900); Chinese striped squirrel]		n/a	[C]	n/a	[P]
Tamiops rodolphei (Milne-Edwards, 1867); Cambodian striped squirrel	NAR	n/a	C	n/a	P
Tamiops sp(p).		C	n/a	C	n/a
Hylopetes sp.; Small flying squirrel		P			
Petaurista elegans (Mueller, 1840); Lesser giant flying squirrel		LF	P	F	
Petaurista philippensis (Elliot, 1839); Indian giant flying squirrel		LF		F	
Rhizomys pruinosus Blyth, 1851; Hoary bamboo-rat				P	
Hystrix brachyura Linnaeus, 1758; Hodgson's porcupine		P			

Threat: GT, Globally Threatened; GNT, Globally Near-Threatened; DD, Data Deficient (all after IUCN 1996); NAR, Nationally At Risk (after SALTER 1993) n/a, species discovered too recently for categorisation. Status: records in brackets are provisional identifications of species; n/a = not applicable; C = common; F = frequent, O = occasional; P = Present, abundance not assessed; L (prefix) = distribution was uneven. 1996 records are based on direct field sightings, except for *Sus* sp., for which one skull was found. 1994 records come mainly from direct observation, with other methods indicated by suffixes: s = sign; d = remains (v = those in village); r = villagers' report.

Mammals from Nakay-Nam Theun NBCA

The total of 37–40 large mammal species living along the Navang road (Tab. 1) is high for a single site in Indochina, rivalling those from several entire NBCAs (approximate totals: Xe Pian NBCA: 37; Dong Hua Sao NBCA: 30; Phou Xang He NBCA: 35; Xe Bang-Nouan NBCA 29; Nam Kading NBCA: 41; Nakay-Nam Theun NBCA: 54; Phou Xiang Thong NBCA 22; Duckworth et al. 1994; Evans et al. 1996; WCS unpubl. data). The richness of carnivores (15 species) and primates (seven) is particularly notable; this is the only Lao site with direct sightings of more than one species of cat or weasel. At least two muntjac species are present.

By day, species such as *Martes flavigula*, *Ratufa bicolor*, monkeys, gibbons and muntjacs were seen more often than at other surveyed sites in Laos. Primates were notably confiding, sometimes allowing the observer under their tree. General hunting pressure on the road is evidently negligable.

Contact frequencies of nocturnal species (Tab. 2) were high, but lower than at two other recently-constructed roads through little-disturbed evergreen forest (Tab. 3, after WCS unpubl. data). This difference is due solely to lorises; when they are excluded from the comparative figures, the Navang road crosses the most productive forest yet surveyed in Laos (Tab. 3). The low hunting pressure (much lower than on these other roads) means that contact frequencies at Nakay-Nam Theun are probably the truest representation of relative species status gained at any Lao site.

Table 2. Nocturnal animals recorded along the two roads.
Figures are for the number of contacts. The number of individuals, where this differed, is in parentheses. c, casual record, not during timed count. Evans (1994) records are from WCS (unpubl. data). Murid rodents and bats are omitted. All unidentified muntjacs were heard and not seen. Ease of survey refers to the ease and detection of mammals, in two categories: those on or near the ground and those in the mid and upper storeys of the trees.

Species	NTX road	NNT road		
		main forest	west forest	Evans (1994)
Nycticebus coucang	1	2	1	1
N. pygmaeus	c	c		
Prionailurus bengalensis		2		
Neofelis nebulosa		1		
Arctogalidia trivirgata		6(8)	2	1
Paguma larvata	4	2		
Paradoxurus hermaphroditus	5	4		1
Prionodon pardicolor		c		1
Viverra zibetha		3	1	
Muntiacus muntjak		1		
Muntjacus/Megamuntiacus sp.	2	1	1	1
Manis pentadactyla	1			
Hylopetes sp.			1	
Petaurista elegans	2	5		1
Petaurista philippensis	3		4	
Rhizmys pruinosus	1			
Hystrix brachyura			1(2)	
Unidentified	1	2	4	3
Hours searching	$39^1/_4$	$45^1/_4$	$14^3/_4$	$8^1/_2$
Total contacts	20	29	15	9
Ease of survey: ground	difficult	easy	easy	easy
Ease of survey: trees	easy	easy	easy	easy

Table 3. Contact frequencies of nocturnal mammals along various roads in Lao through evergreen or semi-evergreen forest surveyed in March–May.
The contact frequency is the no of hours per contact. The lower the figure the more productive the site. All time figures are rounded to the nearest quarter-hour.
Sources: NNT and NTX, this study; T–H, Xe Namnoy, WCS (unpubl. data); Phou Xang He, Duckworth et al. (1994); Phou Xiang Thong, Evans et al. (1996).

Site	Hours effort	Total contacts	Contacts (lorises excluded)	Contact frequency (lorises excluded)
NNT road, main forest	$45^1/_4$	29(31)	27	$1^3/_4$
NNT road, west block	$14^3/_4$	15	14	1
NNT road, 1994	$8^1/_2$	9	8	1
NTX road	$39^1/_4$	20	19	2
Theun-Hinboun access road	$20^1/_2$	19(20)	9(10)	$2^1/_4$
Middle Xe Namnoy road	$12^1/_2$	19(20)	6(7)	2
Phou Xang He Corridor	$78^1/_4$	73	40	2
Phou Xiang Thong	12	13(15)	6(8)	2

The difference in rates between the main forest and the west block (Tab. 3) means little as the latter was visited on only two nights; brief observations in 1994 gave an overall contact frequency in the main forest similar to that in the west block in 1996.

Mammals from Nam Theun Extension

The low species total (18) of large mammals reflects the brevity of the work and the limited observation by day, but it was mirrored by low numbers of individuals (except squirrels) seen by day, and low contact frequencies by night (Tab. 2). These are the lowest for any forest road surveyed in Laos, although discounting lorises the Nam Theun Extension road is as productive as are various other sites (Tab. 3). The scarcity of large mammal sightings here compared with the Nakay-Nam Theun road was reflected in small mammal trapping rates (C. M. Francis pers. comm. 1996). Recording of all mammals was probably hampered by the frequent storms, but it is unlikely that this is the sole explanation for the low sighting and trapping rates.

Altitudinal distribution patterns among mammals in Laos

These roads are the only areas surveyed above 550 m in Laos, but they are in the same catchment so care should be taken when relating to altitude the differences in mammal status between them and lower sites.

Species in the genus *Petaurista* are separated by altitude. In Nakay-Nam Theun, five records of *P. elegans* at 1 000–1 200 m contrasted with four of *P. philippensis* at 700–900 m. In Nam Theun Extension, there were two records of *P. elegans* at 1 000–1 200 m and three of *P. philippensis* at 800–1 000 m. *P. elegans* has not recently been found elsewhere in Laos, but *P. philippensis* occurs widely in lowlands and foothills (Duckworth et al. 1994; WCS unpubl. data). *P. elegans* is primarily montane elsewhere (Payne et al. 1985; Corbet and Hill 1992).

Two geographically sympatric species of pangolin may also be separated altitudinally. The only recent records of *Manis pentadactyla* in Laos are from the Nam Theun Extension and, freshly-caught, in a remote village in Nakay-Nam Theun at 600 m (R. J. Timmins pers. comm. 1997). Pangolins at lower altitude in the Nam Theun catchment (at 380 m in Nam Kading NBCA and at 520 m on the Nakay Plateau; WCS unpubl. data) were *M. javanica* Desmarest, 1822 (Sunda Pangolin).

Paguma larvata, Arctonyx collaris, and *Herpestes urva* were found at one or both sites. Other documented Lao specimens and recent observations of them are also from montane or hill areas (Duckworth 1997), although in other countries they are not always montane: e.g. *P. larvata* occurs commonly at sea-level in Borneo (Payne et al. 1985).

The *Rhizomys pruinosus* is the only recent sighting of a wild or freshly-captured animal in Laos but *R. sumatrensis* (Raffles, 1821) (Large bamboo-rat) has been seen commonly around Vientiane at 200–600 m (Duckworth 1996; WCS unpubl. data). Elsewhere *R. pruinosus* is mainly montane, occurring at 1 000–4 000 m (Corbet and Hill 1992).

Nycticebus coucang was much less common at these two sites than in the lowland sites of Phou Xang He NBCA, the middle Xe Namnoy valley, Nam Kading NBCA and Phou Xiang Thong NBCA (Duckworth et al. 1994; Evans et al. 1996; WCS unpubl. data). It was also scarce on the Nakay Plateau at mid-altitude (520 m) (WCS unpubl. data).

Key species accounts

Species identified provisionally are bracketed. Records are from 1996 unless otherwise stated. Authors are given only for species not in table 1.

Manis pentadactyla – Chinese pangolin
NTX: one at 03h00 on 15 April.

Nycticebus coucang – slow loris
NTX and NNT: small numbers (Tab. 2).

[*Nycticebus pygmaeus* – pygmy loris
NNT and NTX: singles on 13 April* and 20 April* respectively.

There have been few other recent records in Laos (Duckworth 1994 a; Bergmans 1995; WCS unpubl. data; note that the locality of Xe Pian NBCA listed by Bergmans (1995) was erroneous, as a result of poor phraseology in Duckworth 1994 b).]

Macaca arctoides – stump-tailed macaque
NNT: sightings on 8 May* and 13 May* in the main forest probably involved the same troop, of at least 30 animals.

Macaca assamensis – Assamese macaque
NNT: up to two troops observed almost daily in the main forest.

Pygathrix nemaeus – douc langur
NNT: up to two troops (some over 30-strong) observed almost daily in the main forest.

All were the red-shanked (sub)species, *P.* (*n.*). *nemaeus*, as were all other recent Lao records (WCS unpubl. data).

[*Trachypithecus phayrei* – Phayre's langur
NNT: at least two on 8 May* in the main forest.

These were identified as this species rather than as *T. cristatus* (Raffles, 1821) on the basis of latitude (see Fooden 1996; Ruggeri and Timmins 1996).]

Hylobates sp. – gibbon sp.
NNT: up to four groups seen almost daily in the main forest.
NTX: one group seen on 14 April at 09h00. Calling was much less prominent than along the Nakay-Nam Theun road, presumably reflecting a lower population.

On range, these animals are likely to be *H. gabriellae siki* or *H. leucogenys.* The pale patch of fur on the cheeks of males was observed closely but even so conclusive identification was not possible; the taxonomy and distribution of the forms recently recorded in Laos remains unclear (Ruggeri and Timmins 1996).

Prionailurus bengalensis – leopard cat
NNT: two singles (Tab. 2).

Neofelis nebulosa – clouded leopard
NNT: one at 00h50 on 14 May in the forest.

This is the only recent field sighting of the species in Laos. Skins reportedly from the NBCA were seen in Nakay-Nam Theun in 1994 and 1995 (WCS unpubl. data). Villagers' reports (widespread in Laos; Salter 1993; WCS unpubl. data) cannot be confirmed records, and signs are not identifiable with certainty (G. B. Schaller pers. comm. 1996).

Panthera pardus – leopard
NNT: two fighting in a roadside tree at 09h30 on 12 April*. One resting sunlit on the road at 16h00 on 27 April*.

These are the only recent sightings in Laos; the widespread villagers' reports (Salter 1993; WCS unpubl. data) cannot be regarded as confirmed records.

Panthera tigris – tiger
NNT: singles on 11 February (17h00)*, 27 April (15h00)*, and 29 April (08h00), all within 5 km of each other, perhaps involved only one animal.

The first was watching the observer from a crouched position, the second was flushed by the car from its sunlit resting spot, and the third was walking down the road and fled immediately it noticed the observer. These are the only recent field sightings of tiger in Laos, although remains and/or footprints have been seen in a few places, and villagers report the animal widely (Salter 1993; Duckworth et al. 1994; Bergmans 1995; WCS unpubl. data).

Pardofelis marmorata – marbled cat
NNT: one at 14h50 on 9 May.

The only other recent record in Laos is of a freshly-killed animal in the Phongsaly area in early 1996 (W. G. Robichaud pers. comm. 1996). A skin reportedly from Nakay-Nam Theun was seen on the Nakay Plateau in 1995 (WCS unpubl. data).

Mustela strigidorsa – back-striped weasel
NNT: one on 15 April 1994* (Evans et al. 1994).

Only one other recent Lao record was traced by Duckworth (1997).

Prionodon pardicolor – spotted linsang
NNT: one at 21h30 on 11 April 1996* and one at 20h40 on 12 April 1994* (Evans et al. 1994).

These are the only recent field observations from Laos traced by Duckworth (1997); two market specimens from south Laos were mentioned by Bergmans (1995).

Bos frontalis – gaur
NNT: one at 03h30 on 12 May in an area of dense roadside ruderals.

There are only two other recent direct sightings of gaur in Laos (Duckworth et al. 1994; WCS unpubl. data).

Callosciurus inornatus – inornate squirrel
NNT: one at 1 100 m on 17 April 1994*.
NTX: singles on 20 April and 21 April* were separated by at least 2 km.

This squirrel occurs only east of the Mekong; it has not been found commonly at any recently surveyed Lao site (Duckworth et al. 1994; Duckworth 1996; WCS unpubl. data). Although not listed directly as Globally Threatened by IUCN (1996), this source lists Laos within the range of *C. pygerythrus* (I. Geoffroy, 1832); *C. inornatus* was included as a subspecies of the former, which does not otherwise occur in Laos, by Ellerman and Morrison-Scott (1951).

Ratufa bicolor – black giant squirrel
NNT: up to five groups heard daily, with up to three (of 1–2 animals) seen on most days.
NTX: one on 17 April at 910 m*.

At sites across Laos, *Ratufa* seems as susceptible to human pressure as are diurnal primates (Duckworth et al. 1994; Duckworth 1996; WCS unpubl. data) and at these two sites its status again matches that of primates. Furthermore, as with gibbons and monkeys, giant squirrels along the roads were notably easily approached compared with animals at most other Lao sites. The paucity of records from NTX mirrors several other species which were not recorded (notably *Arctogalidia* and monkeys) or scarce (gibbon).

Tamiops rodolphei – Cambodian striped squirrel
NNT and NTX: common in 1994 and presumably in 1996.

These squirrels were not identified to species in 1996; a thorough taxonomic review of the genus in Laos is needed to clarify the number of forms involved and the field characters of each.

Other species of interest

Mustela sibirica – Siberian weasel
NNT: one at 16h00 on 9 May.

No other documented Lao record was traced by Duckworth (1997).

Arctonyx collaris – hog badger
NNT: singles on 27 April at 05h10 and on 2 May at 09h05.
NTX: one at 11h30 on 20 April*.

The only other recent field sightings in Laos traced by Duckworth (1997) are from the Nam Theun catchment at lower altitude.

Muntiacus and *Megamuntiacus* spp. – muntjacs spp.
NNT: nine single muntjacs were observed by day and one at night. Additional animals were heard on most days. One was seen in 1994.
NTX: animals were heard, but by no means daily.

Two muntjac species occur in the Nakay-Nam Theun area in addition to *Muntiacus muntjak*: *Megamuntiacus vuquangensis* and a dark species not yet described to science (Schaller and Vrba 1996; Timmins et al. 1998). Field characters of these two (other than head and antler structure) are based on too few individuals for the range of natural variation within them to be clear. Thus, identifications of the nine animals observed are not yet possible, so descriptions of each are lodged in the WCS Vientiane office to allow possible identification in the future. Two animals of the 11 seen were clearly *M. muntjak* (which occurs in the general area; Timmins et al. 1998), but the other nine lacked the rufous pelage tone diagnostic of this species and at least one had a black dorsal aspect to the tail.

Discussion

Importance of the two areas for mammal conservation

The Navang logging road has the highest recorded species total of any site in the country, the more impressive in view of the relative brevity of the survey. The high sighting rates could reflect genuinely high densities of mammals (and thus a high conservation importance), or they might arise from some other factor (not necessarily indicating real importance of the site), such as the excellent visibility along the road. Some forest animals probably avoid roads but others, e.g. cats, positively select them for transit (e.g. Rabinowitz 1990). On the present survey, resting big cats and foraging civets and muntjacs were clearly associated with the road. Hunting may depress populations and make animals shyer. The low hunting pressure along the road is doubtless important in producing the frequent mammal sightings, but the relative importance of the two effects is unclear.

The high encounter rates along the Navang road stem partly from the excellent viewing, but certainly reflect a community of great conservation importance. Observations at other areas equally as remote, within Nakay-Nam Theun and outside (such as Xe Pian NBCA) would perhaps be equally productive were there barely-used roads into their centres. The results from the Navang road profile an area typical in habitat of much of the Nakay-Nam Theun NBCA, where the road allows a more complete survey than is possible elsewhere.

The Navang road supports at least nine Globally Threatened species, three Data Deficient, six Nationally at risk and probably two muntjac species which, if known prior to publication of IUCN (1996), would have been considered Globally Threatened. It provides the only recent field sightings in Laos by biologists of clouded leopard, marbled cat, leopard, tiger, Siberian weasel, spotted linsang, and an undetermined muntjac. The true significance of these records is obscure, as most of these species cannot be surveyed except by direct sighting or camera trapping; only tigers can be unequivocally identified by signs or villagers' descriptions. The area is also notable for its healthy populations of gibbons, douc langurs, and probably of giant muntjac. By comparison with the data in Schreiber et al. (1989), Nakay-Nam Theun becomes the second most important reserve in the Indomalayan realm for conservation of small carnivores (Duckworth 1997).

The survey of the Nam Theun Extension road was too brief to assess the importance of the area, particularly as human presence is much higher than along the road in Nakay-Nam Theun, but it seems to have a naturally lower density of large mammals.

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Zusammenfassung

Eine Kartierung der Großsäugetierfauna in den zentralen Annamite-Bergen in Laos

Von April bis Mai 1996 wurde eine Kartierung der Großsäugetierfauna in wenig gestörtem, immergrünem Bergwald in und um die Nakay-Nam Theun National Biodiversity Conservation Area (NBCA), Laos, mittels direkter Beobachtung durchgeführt. Die Kartierung erfolgte auf einer Straße, welche wegen des geringen Jagddrucks und der guten Sichtbedingungen die beste Repräsentation des relativen Artenstatus erbrachte, im Vergleich mit allen anderen bislang kartierten Gebieten in Laos. Es wurden mehr Säugetierarten gefunden als in vielen anderen gesamten Regionen der NBCA. Besonders hervorzuheben sind 15 Arten der Ordnung Carnivora. Die nächtlichen Kontaktrate waren höher als in jedem anderen kartierten Gebiet (wenn Plumploris aus dem Vergleich herausgenommen werden). Sichtraten am Tag waren gleichfalls hoch. Insgesamt fielen neun Arten unter die Kategorie „Globally Threatened", drei unter „Data deficient" und sechs unter „Nationally At Risk", was auf eine besondere Bedeutung zur Erhaltung des Gebiets hinweist. Viele dieser Arten weisen große Populationen auf, und einige wurden während eines kürzlich begonnenen Kartierungsprogramms gar nicht gesehen. Auf einer anderen Straße, auf der die Kartierungsbedingungen weniger gut waren, wurden nur einige wenige Arten entdeckt. Im Vergleich mit Kartierungen in Tieflandgebieten und an dem Fuße der bergigen Regionen in Südlaos lassen die Resultate aus der Nakay-Nam Theun National Biodiversity Conservation Area folgende Schlußfolgerungen hinsichtlich der Höhenverteilung der Arten zu: (1) Sympatrische Arten der Gattungen *Petaurista*, *Rhizomys* und *Manis* sind altitudinal getrennt; (2) *Arctonyx collaris*, *paguma larvata* und *Herpestes urva* sind submontan oder montan; (3) *Nycticebus coucang* kommt häufiger im Tiefland als in 1 000 m Höhe war.

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MITTEILUNG DER GESELLSCHAFT

Jochen Niethammer

* 18. 05. 1935
† 02. 01. 1998



JOCHEN NIETHAMMER ist am 2. Januar 1998 verstorben. Er hatte die letzten Jahre im evangelisch-lutherischen Wichernstift Ganderkesee verlebt, nachdem er bereits 1991 bei einem Unfall auf einer studentischen Exkursion eine schwere Hirnverletzung erlitten hatte, die eine Fortsetzung seines bisherigen Lebens unmöglich machte. Alle, die ihn kannten, und sicher mehr noch, die ihm persönlich nahestanden, waren über diesen Schicksalsschlag, der seine wissenschaftliche Tätigkeit abrupt beendete, zutiefst erschüttert. Jetzt muß an ihn, seine Arbeit und seine Verdienste, gerade auch an die um die Deutsche Gesellschaft für Säugetierkunde erinnert werden.

JOCHEN NIETHAMMER wurde am 18. Mai 1935 geboren. Er war der erste von vier Söhnen des Ehepaars Dr. GÜNTHER und RUTH NIETHAMMER, geborene FILTZER. Die Familie lebte zur Zeit der Geburt ihres Sohnes JOCHEN in Berlin. Hier war der Vater am Natur-

kundemuseum der Humboldtuniversität als Ornithologe tätig. Berufliche Veränderungen des Vaters und die Kriegsereignisse brachten für die Familie mehrfache Ortswechsel und für Jochen Niethammer eine Reihe von Schulwechseln mit sich. Aber von 1949 an spielt sich sein Leben, von Unterbrechungen abgesehen, die durch Reisen und Auslandsaufenthalte bedingt waren, in Bonn ab. Sein Vater hatte dort die Leitung der Ornithologischen Abteilung des Museums Alexander Koenig übernommen. Bis 1955, dem Jahr seines Abiturs, besuchte Jochen Niethammer das Ernst-Moritz-Arndt-Gymnasium, um nach der Reifeprüfung an der Bonner Universität sein Studium aufzunehmen. Und zwar studierte er anfänglich Chemie, wechselte aber nach dem Vordiplom entsprechend seiner Neigung und Begabung zur Biologie über. 1964 wurde er an dieser Universität mit der Arbeit „Die Pigmentierung und das Farbmuster junger Haubentaucher", die er bei E. Lubnow anfertigte, promoviert. Mit Ausnahme von zweieinhalb Jahren, die er als Dozent im Rahmen eines Partnerschaftsprojektes an der Universität Kabul in Afghanistan verbrachte, arbeitete er seit der Zeit am Zoologischen Institut der Universität Bonn. 1969 wurde er mit der Arbeit „Zur Frage der Introgression bei Waldmäusen *Apodemus sylvaticus* und *Apodemus flavicollis* (Mammalia, Rodentia)" habilitiert und bereits 1971 zum außerplanmäßigen Professor ernannt. Von 1973 an lehrte Jochen Niethammer als wissenschaftlicher Rat und Professor an seiner Universität Vergleichende Anatomie und Systematik.

Das tief verwurzelte Interesse Jochen Niethammers an der belebten Natur, insbesondere an den Säugetieren, war früh erkennbar. Bei diesem zeitigen Interesse spielten sicher der Vater und die Lebensumstände der Familie eine fördernde Rolle. Als Schüler schon sammelte und präparierte er Kleinsäuger und berichtete bereits im Alter von 18 Jahren in seiner ersten Veröffentlichung über den Erstfund einer Sumpfspitzmaus im Rheinland. Später führten ihn Forschungs- und Sammelreisen in viele Länder. Das während solcher Reisen und der Auslandsaufenthalte gesammelte Material, insbesondere das aus Afghanistan, und die sich bei seiner Bearbeitung ergebenden Fragen und Probleme waren Grundlage für zahlreiche Publikationen. In ihnen wie in dem gesamten Werk Jochen Niethammers und seiner vielen Schüler spielten Fragestellungen zur Faunistik, Systematik, Morphologie, Biologie und Evolution von Nagetieren und Spitzmäusen eine zentrale Rolle. Beispielhaft seien die zahlreichen Aufsätze über die Säugetierfauna Afghanistans, die Bearbeitung der Proteinvariation der Waldmaus und die vielen monographischen Darstellungen einzelner Arten herausgegriffen. Die umfangreiche Publikationsliste (s. Rainer Hutterer: Jochen Niethammer, Biographie und Bibliographie, Bonn. Zool. Beitr. **46**, 1996) läßt nicht nur seine Vielseitigkeit und wissenschaftlichen Vorlieben ungewöhnlich klar erkennen, sondern sie verdeutlicht auch, daß Jochen Niethammer seine wissenschaftliche Linie konsequent verfolgte, ja, daß er sich in Selbstbescheidung auch dem Kleinen, Unspektakulären zuwenden konnte. Karrierebeflissenheit um jeden Preis war ihm fremd.

Große Energien hat Jochen Niethammer in die Herausgabe wissenschaftlicher Werke investiert. Hier muß vor allem das mit F. Krapp zusammen herausgegebene Handbuch der Säugetiere Europas genannt werden. Es ist mit seinen inzwischen neun Bänden ein Standardwerk hoher Reputation und aus den Bibliotheken der Säugetierkundler nicht mehr wegzudenken. Jochen Niethammer war ferner Mitherausgeber des Handbuches der Zoologie (Band 8, Mammalia) und – dies ist hier von besonderem Interesse – seit 1973 der Zeitschrift für Säugetierkunde. Für unsere Zeitschrift wurde er über viele Jahre von allen Herausgebern für die Begutachtung eingehender Manuskripte am intensivsten beansprucht. Seine Gutachten waren bei selbstverständlicher Kompetenz unglaublich detailliert und präzise, und dabei immer hilfreich für Autor und die Zeitschrift. Diese hingebungsvolle Herausgebertätigkeit hat das Ansehen der Zeitschrift für Säugetierkunde nachhaltig geprägt und vor allem mit ihr hat sich Jochen Niethammer um unsere Gesellschaft verdient gemacht.

Die Deutsche Gesellschaft für Säugetierkunde schuldet JOCHEN NIETHAMMER, der ab 1958 ihr Mitglied war, aber nicht nur für diese Arbeit Dank, sondern ebenso für seine Tätigkeit in ihrem Vorstand. Er war von 1972 bis 1981 Schriftführer der Gesellschaft und danach für eine Amtsperiode von 1982 bis 1986 ihr 3. Vorsitzender.

Es erstaunt nicht, daß JOCHEN NIETHAMMER mit seinen großen, nicht auf die Säugetierkunde beschränkten Kenntnissen sowie seinem vorbehaltlosen und vielseitigen Engagement bei Kollegen hohe Achtung genoß und von seinen Studenten bewundert wurde. Seine Autorität aber war ausschließlich durch wissenschaftliche Fähigkeiten und menschliche Qualitäten begründet. Unter ihnen haben Liebenswürdigkeit, persönliche Bescheidenheit und Offenheit ihm sehr viele Sympathien gewonnen.

Für all dies ist JOCHEN NIETHAMMER großer Respekt zu zollen und aufrichtig zu danken. Er hat für seine Kollegen und Studenten, für die er jederzeit zu sprechen war, eine große Lücke hinterlassen.

H. SCHLIEMANN, Hamburg

Z. Säugetierkunde **63** (1998) 254–256
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INTERNATIONAL JOURNAL
OF MAMMALIAN BIOLOGY

Buchbesprechungen

Kleiman, D. G.; Allen, M. E.; Thompson, K. V.; Lumpkin, S. (eds.): **Wild Mammals in Captivity.** Principles and Techniques. Chicago and London: The University of Chicago Press 1996. 639 pp., 55 Tabs., 103 Figs., USD 70.–, ISBN 0-226-44002-8

This book is intended to serve as a handbook on issues relevant for keeping and breeding wild mammals in captivity. It is divided into seven parts, and each part consists of a number of chapters written by different authors. Part one is devoted to basic husbandry, and the respective chapters are addressing ethical and welfare issues, preventive medicine, methods of capture and anesthesia, neonatal care, identification and marking, introduction and socialization, animal learning and husbandry, and zoo security and dealing with escaped animals. Part two concentrates on nutrition, and apart from general outlines on nutrition in zoos and on essential nutrients in mammalian diets, the feeding and nutrition of herbivores, carnivores, and omnivores (especially primates) are treated in separate chapters. Part three is dealing with exhibitry, and there are chapters on the bio-park concept, education through exhibit design, horticultural philosophies, structural environmental enrichment, and the maintenance of water quality in aquatic mammal exhibits. Part four contains chapters on population management for conservation. Problems of units of management in conservation (species, subspecies, races), genetic research and its application in zoos, demographic and genetic management of captive populations, captive management in relation to dispersal, issues of surplus animals, reintroduction programs, and the role of conservation and survival centers in wildlife conservation are addressed. Part five focuses on behaviour. Effects of captivity on the behaviour of wild mammals, communication and social behaviour, social organization and mating systems, behavioural development and play, and the ecology and psychology of feeding and foraging are considered. Part six is concerned with reproduction. Chapters deal with reproductive behaviour, reproductive physiology, female reproductive parameters, male reproduction, contraception as a management tool, pregnancy and parturation in captive mammals, parental care, and patterns of growth. Part seven is devoted to captive mammal research, and chapters deal with various aspects of research activities in zoos. The book is completed by altogether five appendices, providing information on mammalian phylogeny, articles and literature on captive management, US wildlife regulations applicable to zoos, records, studbooks, and ISIS inventories, and inter-zoo breeding loans.

All the respective chapters are written by experts in their field, and despite being presented in a concise style provide a wealth of information and practical advice. In each chapter a number of subheadings are used to facilitate access to the various items addressed. Tables, figures, and occasional chapter appendices are well organized, and the respective reference sections contain a well balanced number of recent citations. Altogether this book can be warmly recommended to managers of captive populations in zoos and reserves, and to students and researchers of mammalian conservation biology.

G. B. Hartl, Kiel

Storch, V.; Welsch, U.: **Systematische Zoologie.** 5. Aufl. Stuttgart: Gustav Fischer Verlag 1997. 804 S., 448 Abb., 88,– DM. ISBN 3-473-25160-0.

Die „Systematische Zoologie“, ein Standardlehrbuch für Studierende der Zoologie, ist nunmehr in der fünften Auflage erschienen. Auffallend ist das neue Gesicht des Einbandes, durch dessen geschmackvolle, mehrfarbige Gestaltungsweise mit Tierbildern und Lebensraumdarstellungen der Gustav Fischer Verlag das Buch für den bibliophilen Leser schon rein äußerlich sehr attraktiv gemacht hat. Die Gliederung des Werkes nach einzelnen Tiergruppen wurde beibehalten. Dieser Aufbau stellt das Buch als taxonomisch geordnetes Nachschlagewerk dem hauptsächlich nach zoologischen Disziplinen, Funktionskreisen bzw. Organen gegliederten „Kurzen Lehrbuch der Zoologie“ zur Seite, das von denselben Autoren im selben Verlag vorliegt.

In einem einführenden Abschnitt werden wichtige Grundlagen der Systematik und Taxonomie kurz und anschaulich dargestellt. Bis zur Ebene der Ordnung finden sich dann durchgehend für jede

Tiergruppe eine geraffte Darstellung der Anatomie sowie Bemerkungen zur Taxonomie, zur Lebensweise und zur Fortpflanzung. Die jeweils vorhandenen Familien werden vorgestellt und einzelne Vertreter bis zur Gattung oder Art hin charakterisiert. Die bereits in vorhergegangenen Auflagen zahlreichen und sehr klaren Abbildungen wurden in mehreren Fällen weiter verbessert. Als Neuheit werden die biologischen und ökologischen Besonderheiten von etwa 300 für den Menschen bedeutsamen Arten in grau unterlegten Kästen etwas eingehender beschrieben. Ebenso finden sich bildliche Darstellungen von etwa 200 Tierarten in ihrem Lebensraum. Die entsprechenden Tafeln sind von hervorragender Abbildungsqualität und sehr übersichtlich beschriftet. Bei einigen Tiergruppen stärker ins Detail gehende Bemerkungen zur Phylogenie runden zusammen mit entsprechenden Stammbäumen das Werk ab.

Insgesamt präsentiert sich die „Systematische Zoologie" als eine sehr ausgewogene Darstellung des Tierreiches. Neben einem taxonomischen Überblick und einer vergleichend-anatomischen Charakterisierung wird dem Leser auch Einblick in die biologischen Besonderheiten sowie die ökologische Vergesellschaftung der einzelnen Tiergruppen geboten. Sowohl dem Studenten der Biologie als auch dem interessierten Laien steht damit ein didaktisch hervorragend aufbereiteter Einblick in die Tierwelt zur Verfügung. Dem Lehrenden an Hochschulen und Gymnasien wird das Buch weiterhin als unersetzliches Nachschlagewerk dienen.

G. B. Hartl, Kiel

Software-Besprechung

Expert Center for Taxonomic Identification – ETI (Hrsg.): Marine Mammals of the World. CD-ROM, Windows Version. Berlin: Springer-Verlag 1996. DM 110,–. ISBN 3-540-14508-7.

Diese CD-ROM basiert auf einem von der FAO in Buchform herausgegebenen „Species Identification Guide". Die Daten wurden aktualisiert und durch Farbabbildungen und Filmszenen ergänzt. Es werden nicht nur Beschreibungen der 119 Arten (Cetacea, Pinnipedia, zwei Vertreter der Mustelidae [*Enhydra lutris* und *Lutra felina*] und ein Repräsentant der Ursidae [*Ursus maritimus*]) geboten, auch wird deren Verbreitung in den verschiedenen von der FAO definierten Fischfang-Zonen dargestellt. Ferner wird anhand einer vom „Expert Center for Taxonomic Identification – ETI" der Universität Amsterdam entwickelten biogeographischen Datensammlung das Auftreten von Meeressäuger-Arten in Planquadraten der Ozeane und Randmeere dokumentiert. Es ist möglich, Daten und Abbildungen zu exportieren. Bei den speziellen Angaben zu den Arten ist jeweils ein „Schalter" vorhanden, der auf spezifische Literatur hinführen soll, doch ließ sich bei entsprechenden Versuchen auch bei wohlbekannten Arten kein Literaturzitat finden!

Der Referent fragt sich, ob eine gedruckte Version dieser Publikation mit qualitativ hochwertiger Farbwiedergabe der Abbildungen die Aufgaben eines solchen Werkes nicht besser erfüllen könnte; die Benutzbarkeit eines Druckwerkes ist fast überall ohne weitere Hilfsmittel möglich, für die vorliegende CD-ROM ist ein Computer erforderlich. Nicht jede technische Neuerung stellt in allen Teilbereichen die überzeugendste Lösung bei der Bearbeitung wissenschaftlicher Fragestellungen dar!

P. Langer, Gießen

Moeller, H. F.: **Der Beutelwolf *Thylacinus cynocephalus***. Die Neue Brehm-Bücherei, Bd. 642. Magdeburg: Westarp Wissenschaften 1997. 195 pp., 127 Abb., 11 Tab. DM 44,–. ISBN 3-89432-869-X.

Bereits vor mehr als dreißig Jahren hat der Autor des vorzustellenden Buches Daten über den vermutlich 1936 ausgestorbenen Beutelwolf gesammelt. Die ersten Ergebnisse seiner Studien wurden 1968 veröffentlicht. Neben der Beschäftigung mit anderen säugetierkundlichen Themen blieb H. F. Moeller der Erforschung von *Thylacinus cynocephalus* treu und untersuchte nicht nur das in europäischen Sammlungen verfügbare Material, sondern auch die Bestände in Nordamerika und in Australien. Er stellt in dem vorliegenden Buch nicht nur die Ergebnisse seiner Studien vor, sondern macht auch Informationen von Zeitzeugen und aus der australischen Presse verfügbar. Weiterhin bietet er eine bemerkenswerten Fülle meist historischer Photos des Beutelwolfes.

Es muß jeden an der Säugetierkunde Interessierten mit Bedauern erfüllen, daß trotz dieses langanhaltenden und engagierten Einsatzes in diesem „Nachruf" nur noch ein unvollständiges Bild der Biologie dieses Raubbeutlers zusammengestellt werden konnte und neuere physiologische Befunde sowie ebensolche Ergebnisse von Studien zur inneren Anatomie weitgehend fehlen. Es werden allerdings Angaben zum Skelett und zum Gehirn gemacht und zu Brust- und Baucheingeweiden einige grundlegende Informationen gegeben. Es ist dem Autor in Anbetracht der ungünstigen Materialsituation als hohes Verdienst anzurechnen, über Gestalt und Anatomie, Biologie und Verhalten, ja sogar über frühe pathologische Befunde Daten aus wissenschaftlichen und journalistischen Quellen zusammengestellt zu haben, so daß dem Leser ein anschauliches Bild dieser höchstwahrscheinlich für immer verlorenen Beuteltierart geboten wird. Angaben zu angeblichen Sichtungen von *Thylacinus cynocephalus* nach 1936, dem Jahr des Todes des letzten bekannten Individuums, sowie zur Haltung in menschlicher Obhut vor diesem Zeitpunkt werden ebenfalls geboten. Ein zehnseitiges, materialreiches Literaturverzeichnis belegt die Quellen, welche für diese informative Zusammenstellung und Analyse herangezogen wurden.

P. Langer, Gießen

Koenigswald, W. von; Storch, G. (Hrsg): **Messel – Ein Pompeji der Paläontologie**. Reihe Species, Bd. 2, Sigmaringen: Thorbecke Verlag 1998. 159 pp. DM 59,80.

Die Herausgeber haben mit diesem Werk nicht nur eine ganze Reihe kompetenter Autoren vereint. Vielmehr ist dieser Bildband mit seinen hervorragenden, großformatigen über 55 Farbfotos der weltweit herrausragenden messelschen Funde eine neue Fundgrube ganz anderer Art. Darüber hinaus vervollständigen rasterelektronenmikroskopische Bilder und wenige Graphiken den Band. Dieses prächtige Buch sollte von möglichst vielen Biologen wahrgenommen werden, insbesondere natürlich von Säugetierkundlern, denn die Mehrzahl der Darstellungen bezieht sich auf Mammalier. Durch die Breite der behandelten Funde und die überwiegend ausgezeichneten Texte von 25 Autoren erhält man einen tiefen Einblick und eine breite Gesamtschau über die Fauna des Eozäns unserer Region. So wird einer der beiden Primatenfunde des Buches, *Europolemur*, mit einem wahrlich sensationellen Röntgenbild des Schädels gezeigt, in welchem der Zahnwechsel dieses Primatengebisses in allen Einzelheiten zu sehen ist. Oder: Wer hätte jemals mit *Heterohyus* und seinen erstaunlichen Konvergenzen zur Adaptation an die Spechtnische von *Daubentonia* gerechnet?

Das Buch ist eine Art Kaleidoskop, und so mag man vermissen, daß es weder einer taxonomischen noch einer sonstwie faßbaren Systematik folgt: eine Ichneumonide zwischen dem berühmten Adapiden und einer Ralle.... Trotzdem! Man kann dieses herrliche Buch nur jedem an Evolution Interessierten empfehlen.

C. Niemitz, Berlin

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c) From reference books:

Niethammer, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

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On biochemical genetic variability and divergence of the two Hedgehog species *Erinaceus europaeus* and *E. concolor* in central Europe

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Abstract

Allozymic variation within and between the two closely related hedgehog species *Erinaceus europaeus* (n = 45) and *E. concolor* (n = 40) from their central European contact and overlap zones was studied. Horizontal starch gel electrophoresis of 27 isozyme systems encoding for 37 putative loci was employed, using kidney tissue samples. Average heterzygosity (H_e = 0.019–0.02 in *E. europaeus*; H_e = 0.000–0.02 in *E. concolor*) and rates of polymorphism ($P_{99\%}$ = 5.41 in *E. europaeus*; $P_{99\%}$ = 2.7–5.41 in *E. concolor*) of regional samples were low as compared to mammalian standards. Three loci (Aat-1, Aat-2, Gpi) showed obviously alternately fixed (differential diagnostic) alleles between the two species. There was no indication of introgressive hybridization. Despite low levels of intraspecific genetic distances (Nei's unbiased D for *E. europaeus* = 0.003; and for *E. concolor* = 0.000–0.005), significant substructuring of the gene pools of either species was found. Based on the interspecific genetic distance (Nei's unbiased D = 0.087–0.099), the estimated period of cladogenetic separation amounts to 435,000–495,000 years BP. This accords with the hypothesis of the evolution of the two species during the Pleistocene.

Key words: *Erinaceus europaeus*, *Erinaceus concolor*, hedgehogs, allozymes, electrophoresis

Introduction

The two closely related hedgehog species *Erinaceus europaeus* and *E. concolor* show allopatric occurrence over most parts of their distributional ranges (Reeve 1994). In central Europe, however, a zone of overlap exists in Poland, the Czech Republic, Austria, and Italy (Kratochvíl 1966; Rödl 1966; Kratochvíl 1975; Bauer 1976; Pucek and Raczyński 1983; Lapini and Perco 1987; Filippucci and Lapini 1988). F_1- and F_2-hybrids between the two species as well as backcrosses have been produced in captivity (e.g., Herter 1935; Poduschka and Poduschka 1983), and, according to morphological studies, may occasionally occur in the wild (Herter 1934; Holz 1978; Ansorge 1987).

The central European region of sympatric occurrence provides an opportunity to compare the level of interspecific gene pool divergence to the genetic variability of either species within a restricted geographical range. Given there is no substantial introgression, gene pool divergence between the two species in their overlap zone is expected to be clearly greater than between conspecific regional samples, even if the latter are compared between more distant sites (Avise 1975; Nei 1987).

Material and methods

Specimens of the western European hedgehog (*Erinaceus europaeus* L., 1758, n = 45) and the eastern European hedgehog *Erinaceus concolor* Martin, 1838, n = 40) were collected as road kills in the Upper Lusatia (Oberlausitz) region (eastern Germany, see also ANSORGE 1987) and in various parts of Austria between June 1987–June 1997. Sampling locations of some of the Austrian specimens were reported in SPITZENBERGER (1995) and EGERMANN (1996). Species determination was carried out using morphological criteria (cf., HERTER 1934; KRATOCHVÍL 1975; WOLFF 1976). There were no problems with species determination of any individual by using morphological criteria (metric and nonmetric skull and mandible characters, head and ventral coat colouration and pattern). Details of sampling localities are given in figure 1. Specimens of *E. europaeus* were grouped into two regional samples: Upper Lusatia (EE-UL, n = 40) and Austria (EE-A, n = 5). Specimens of *E. concolor* were grouped into three regional samples: Austria, north of the river Danube (EC-ND, n = 11), Austria, south of the river Danube but north of the Alps (EC-SD, n = 24), and Austria/Carinthia (Kärnten, south of the main Alpine range) (EC-C, n = 5). Apart from this regional grouping, all specimens found within or at the edge of the Austrian overlap zone (Lower and Upper Austria, n = 15) were considered in a second approach for an inter-specific comparison. Their morphological features did not provide any ambiguity in species determination. Four of these hedgehogs were determined morphologically as *E. europaeus* and 11 as *E. concolor*.

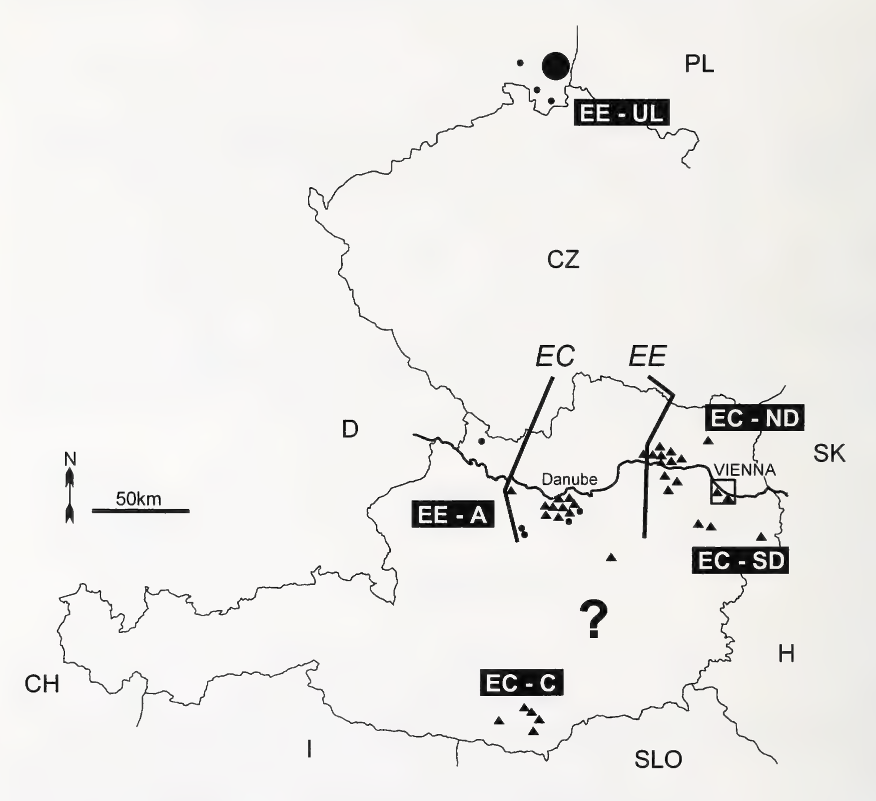


Fig. 1. Sampling localities of western (circles) and eastern (triangles) European hedgehogs in Austria and eastern Germany.
One or more individuals per symbol. The two vertical lines in Austria delineate the eastern edge of the range of the western European hedgehog (EE), and the western edge of the range of the eastern European hedgehog (EC) in the provinces of Upper and Lower Austria (cf. BAUER 1976). The question mark indicates absence of published data on distribution in this part of Austria. Acronyms of regional samples of western European hedgehogs: EE-UL = Upper Lusatia (most from Görlitz and environs), EE-A = Austria; of eastern European hedgehogs: EC-ND = Austria north of the river Danube; EC-SD = south of the river Danube; EC-C = southern Austria, province of Carinthia.

Kidneys of all hedgehogs were stored at –20 °C until processed. Preparation of kindey tissue samples, electrophoresis, and protein-specific staining were performed according to Hartl and Höger (1986) and Grillitsch et al. (1992). Isozyme loci were designated by numbers starting with "1" as the most anodal (cf., e.g. Rothe 1994). For resolving allelic variants migrating allozymes of individuals of both species were compared side-by-side on the same gels. Letters with negative signs denoted cathodal migrating allozymes. Genetic interpretation of electromorphs followed the principles given in Rothe (1994).

The following 27 isozyme systems encoded by 37 presumptive structural gene loci were assayed for allozymic variation by horizontal starch gel electrophoresis (isozyme/-system, abbreviation, E.C. number, and corresponding structural gene loci in parentheses): sorbitol dehydrogenase (SDH, 1.1.1.14, Sdh), lactate dehydrogenase (LDH, 1.1.1.27, Ldh-1, -2), malate dehydrogenase (MOR, 1.1.1.37, Mor-1, -2), malic enzyme (MOD, 1.1.1.40, Mod-1, -2), isocitrate dehydrogenase (IDH, 1.1.1.42, Idh-1, -2), glucose dehydrogenase (GDH, 1.1.1.47, Gdh), glutamate dehydrogenase (GLUD, 1.4.1.3, Glud), NADH-diaphorase (DIA, 1.6.2.2, Dia-1, -2), superoxide dismutase (SOD, 1.15.1.1, Sod-1), purine nucleoside phosphorylase (NP, 2.4.2.1, Np), aspartate aminotransferase (AAT, 2.6.1.1, Aat-1, -2), glutamate pyruvate transaminase (GPT, 2.6.1.2. Gpt), hexokinase (HK, 2.7.1.1, Hk-1), creatine kinase (CK, 2.7.3.2, Ck-2), adenylate kinase (AK, 2.7.4.3, Ak-1, -2), phosphoglucomutase (PGM, 2.7.5.1, Pgm-1), esterases (ES-D, 4.2.1.1, Es-D), acid phosphatase (ACP, 3.1.3.2, Acp-1, -2), fructose-1,6-diphosphatase (FDP, 3.1.3.11, Fdp), β-galactosidase (β-GAL, 3.2.1.23, β-Gal), peptidases (PEP, 3.4.11, Pep-1, -2), aminoacylase (ACY, 3.5.1.14, Acy), adenosine deaminase (ADA, 3.5.4.4, Ada-1), fumarate hydratase (FH, 4.2.1.2, Fh-1, -2), aconitase (ACO, 4.2.1.3, Aco-1), mannose phosphate isomerase (MPI, 5.3.1.8, Mpi), glucose phosphate isomerase (GPI, 5.3.1.9, Gpi).

The BIOSYS-1 pc package (Swofford and Selander 1989) was used to calculate allele frequencies, average heterozygosity (H_o – observed, H_e – expected), proportion of polymorphic loci (P, 99% criterion), mean number of alleles per locus (A), deviation of observed genotypes at polymorphic loci from Hardy-Weinberg expectations by calculating exact significance expectations and pooling of genotypes of loci with more than two alleles, F-statistics for estimation of partitioning of relative genetic variability, genetic distances (Nei's (1978) D and Rogers' distances), and to summarize genetic relationships between regional samples by cluster analyses (UPGMA dendrogram and Wagner unrooted tree). Heterogeneity of allele frequencies at polymorphic loci across the respective geographical samples of *E. europaeus* and *E. concolor* was proved by Fisher's exact test and the G-test.

Results

A total of 2750 genes of *E. europaeus* and of 2908 genes of *E. concolor* were analyzed by means of their products (proteins). Allelic variation was observed at six loci (Tab. 1). However, polymorphism was found only at the Mor-2 and the Pep-1 loci in *E. europaeus*, and at the Gpi and the Pep-1 loci in *E. concolor.* At the Aat-1, Aat-2, and Gpt loci alleles were obviously alternately fixed for the two species. Allele frequencies, observed and expected heterozygosity, rate of polymorphism and average number of alleles per locus are listed in table 1, separately for each regional sample. There was no significant deviation of genotype frequencies from Hardy-Weinberg expectations at any polymorphic locus. The frequencies of the Mor-2 alleles varied significantly ($p = 0.026$; d. f. = 1, Fisher's exact test) between the two regional samples of western European hedgehogs. In eastern European hedgehogs the Pep-1 allele frequencies varied significantly ($p < 0.025$, d. f. = 2; G-test) across the three regional samples.

A summary of the non-hierarchical F-statistics is presented in table 2, separately for each species. Values of Wright's (1978) hierarchical F-statistics for estimating the relationship between intra- and interspecific partitioning of the relative genetic variability are given in table 3. The matrices of pairwise Nei's (1978) genetic distances and Rogers' distances are given in table 4. Genetic relationships among all hedgehog samples are depicted in figure 2 by a UPGMA dendrogram based on Nei's (1978) D values and in figure 3 by a Wagner unrooted tree using Rogers' distances and midpoint-rooting of the longest path.

Table 1. Genetic variation in *Erinaceus europaeus* and *E. concolor.* Allele frequencies at variable/polymorphic loci, observed (H_o) and expected (H_e) heterozygosity, rate of polymorphism (99% criterion) (P), and mean number of alleles per locus (A) are given for each regional sample. n = number of hedgehogs. For regional sample acronyms, see Material and methods.

Locus		*E. europaeus*			*E. concolor*	
		UL	A	ND	SD	C
n	allele	40	5	11	24	5
Mor-2	a	0.421	0.800	1.000	1.000	1.000
	b	0.579	0.200	0.000	0.000	0.000
Aat-1	a	1.000	1.000	0.000	0.000	0.000
	b	0.000	0.000	1.000	1.000	1.000
Aat-2	-a	1.000	1.000	0.000	0.000	0.000
	-b	0.000	0.000	1.000	1.000	1.000
Gpt	a	1.000	1.000	0.000	0.000	0.000
	b	0.000	0.000	1.000	1.000	1.000
Pep-1	a	0.857	0.800	0.636	0.587	1.000
	b	0.125	0.200	0.364	0.413	0.000
	c	0.018	0.000	0.000	0.000	0.000
Gpi	-a	1.000	1.000	1.000	0.870	1.000
	-b	0.000	0.000	0.000	0.130	0.000
H_o		0.014	0.011	0.015	0.015	0.000
H_e		0.020	0.019	0.013	0.020	0.000
P (%)		5.410	5.410	2.700	5.410	0.000
A		1.080	1.050	1.030	1.050	0.000

Table 2. Polymorphic loci and WRIGHT'S (1978) non-hierarchical F-coefficients for *Erinaceus europaeus* and *E. concolor*

Locus	*E. europaeus*			*E. concolor*		
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
Mor-2	0.244	0.552	0.407	–	–	–
Pep-1	–0.030	–0.007	0.021	0.012	0.186	0.177
Gpi	–	–	–	0.233	0.303	0.091
mean:	0.090	0.308	0.239	0.054	0.207	0.161

Table 3. variance components and WRIGHT'S (1978) hierarchical F-statistics combined across loci for *Erinaceus europaeus* and *E. concolor.*

Comparison (X/Y)	Variance component	F_{XY}
regional sample/species	0.103	0.161
regional sample/total	1.570	0.747
species/total	1.468	0.698

Table 4. Pairwise genetic distances between intraspecific regional or species samples. NEI'S (1978) D above and modified Rogers' distances (WRIGHT 1978) below diagonal. For sample acronyms, see Fig. 1.

	(1)	(2)	(3)	(4)	(5)
EE-UL (1)		0.003	0.097	0.099	0.096
EE-A (2)	0.063		0.087	0.088	0.087
EC-ND (3)	0.303	0.288		0.000	0.003
EC-SD (4)	0.304	0.290	0.023		0.005
EC-C (5)	0.301	0.289	0.060	0.071	

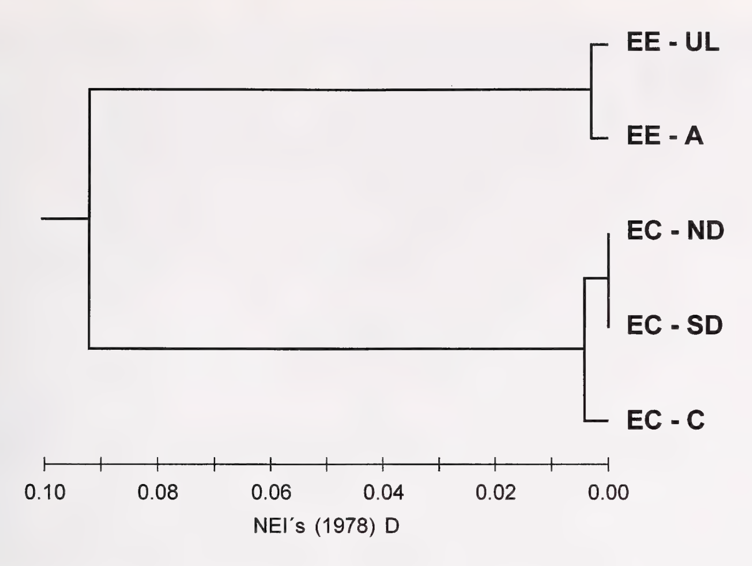


Fig. 2. UPGMA dendrogram depicting genetic relationships among the regional samples of western and eastern European hedgehogs. Cophenetic correlation index = 0.996.

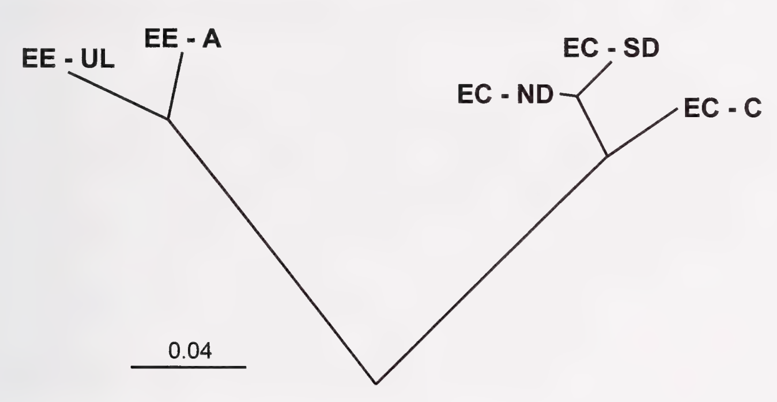


Fig. 3. Wagner dendrogram based on modified Rogers' distances, and rooted by the midpoint of the longest path. Total length of the tree = 0.374; cophenetic correlation coefficient = 1.0.

Regarding the 15 hedgehogs from the overlap zone, there was no indication of introgressive hybridization; species designation by allozymes was consistent with the determination using morphological criteria in each individual. The genetic distances between the two species based on these individuals from the overlap zone (Nei's (1978) D = 0.087; Rogers' distance = 0.289) conformed with the other values of interspecific divergence listed in table 4.

Discussion

Genetic variability within either species was rather low, as compared to mammalian standards (e.g, Nevo et al. 1984; Tolliver et al. 1985; Tiedemann et al. 1996). Nevertheless, the significant variation of allele frequencies at the polymorphic loci in both species indicates some substructuring of their respective gene pools. In *E. europaeus*, the Mor-2^b allele was

currently present only in hedgehogs from north of the river Danube. Among the eastern European hedgehogs, the Pep-1^b allele occurred only in the region south of the river Danube and north of the main Alpine range. These statistically significant findings do not prove the absence of these two genetic variants from outside of the specified regions, but they indicate at least a somewhat reduced gene flow across regions. This is also revealed by the respective fixation indices (F_{ST}); they are within the upper range of values commonly encounterd for genetic partitioning among mammalian populations (cf., AVISE 1994). Based on the relationship between the number of migrants (N_m) and the fixation index ($N_m \approx (1 - F_{ST})/4F_{ST}$; WRIGHT 1943), applying to the island model of populations, an average of 0.796 western European hedgehogs per generation exchange their genes between the two regions Upper Lusatia and Austria. The respective value for the eastern European hedgehogs amounts to $N_m \approx 1.303$. The first value is below the level necessary to balance genetic drift between populations, the latter is slightly above (cf., ALLENDORF 1983).

The genetic distances between the two hedgehog species *Erinaceus europaeus* and *E. concolor*, from portions of their distributional overlap and contact zones in central Europe, are within the range commonly observed among congeneric mammalian species; NEI's (1978) D values are, however, close to the lower limit (e.g., SHOTAKE et al. 1977; AVISE and AQUADRO 1982; NEI 1987; FILIPPUCCI et al. 1991; JANECEK et al. 1991; GRILLITSCH et al. 1992; ROGERS and ENGSTROM 1992; AVISE 1994); they are lower than those usually encountered in insectivores, when similar numbers of allozyme loci were studied (e.g., FILIPPUCCI et al. 1987; RUEDI et al. 1993; SUCHENTRUNK et al. 1995). Nevertheless, distinct gene pool separation between the two species in the study areas is revealed by most probably, alternately fixed (diagnostic) alleles at three loci (Aat-1, -2, Gpt). The presently found interspecific genetic distances are by far greater (by ca. 20 times for Nei's D, and by ca. 4 times for Rogers' distances) than all those obtained between regional samples of either species. Correspondingly, the overall genetic variability presently encountered in the hedgehogs is mainly partitioned between the two species (69.8%), and to a clearly lesser degree (16.1%) among intraspecific regional samples.

All 15 hedgehogs from the sympatric range could be unambiguousely classified as either *E. europeaus* or *E. concolor* by their respective allozyme pattern. In each specimen there was concordance between allozymic and morphological species diagnosis. As already found in the overlap zone in north-eastern Italy (FILIPPUCCI and LAPINI 1988), there was presently no suspect of introgressive hybridization. However, a much larger sample from the overlap zone has to be studied to exclude the occurrence of occassional hybridization.

The presently encountered level of interspecific genetic differentiation (NEI's (1978) D = 0.087–0.099) is clearly lower than in the Italian section of the species' overlap zone (NEI's (1972) D = 0.212; FILIPPUCCI and LAPINI 1988). This difference may be due to the different numbers of loci screened, the different tissues used (mainly skeletal muscle in FILIPPUCCI and LAPINI 1988), or different biochemical conditions of electrophoresis (NEI 1987). FILIPPUCCI and LAPINI (1988) based their calculations of interspecific genetic divergence on 25 loci. Among these, α-Gpdh, Me (synonymous to Mod, E.C. 1.1.1.40), and Est-3 revealed most probably, alternately fixed alleles between their two species samples; these loci contributed most to interspecific genetic distance. While α-Gpdh was not screened presently, there was no allelic variation at the two Mod loci in our study. Moreover, because of ambiguous electromorphic patterns, we refrained from assigning genotypes at esterase loci in our samples. Hence, the presently found lower genetic distance values may result particularly from the exclusion of these polymorphic loci of FILIPPUCCI and LAPINI (1988). However, the calculation of genetic distances has been presently based on 37 loci, which is sufficient for reliable estimates of genetic distances, even when gene pool divergence is shallow (NEI 1987).

Dating the cladogenetic event that lead to the two modern hedgehog species *E. europaeus* and *E. concolor*, based on NEI's (1978) D and the average rate of codon substitution ($\alpha = 10^{-7}$, NEI 1975), resulted in a divergence time of 435,000–495,000 years BP. This estimate of speciation time is somewhat below that suggested by FILIPPUCCI and LAPINI (1988). Nevertheless, both estimates are in good accordance with the (paleontologically unproved) hypothesis of the separation of an ancestral European hedgehog genepool in south-eastern and south-western European refuge areas during the Pleistocene, with subsequent independent evolution and a secondary invasion of both species into central Europe during the Holocene (HERTER 1934).

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Zusammenfassung

Zur biochemisch-genetischen Variabilität und Divergenz der beiden Igelarten Erinaceus europaeus und E. concolor in Mitteleuropa

Untersucht wurde die Allozym-Variabilität der Igelarten *Erinaceus europaeus* (n = 45) und *E. concolor* (n = 40) aus ihrem sympatrischen und parapatrischen Vorkommen in Mitteleuropa, sowie ihre genetische Differenzierung mittels horizontaler Stärkegelelektrophorese. Sechs der 37 Strukturgenloci zeigten allelische Variabilität, wobei an drei Loci (Aat-1, Aat-2, Gpi) zwischen den beiden Arten alternativ fixierte (differenzialdiagnostische) Allele vorlagen. Bei jedem Individuum stimmten morphologische und biochemisch-genetische Artdiagnose überein. Es konnte kein Hinweis auf introgressive Hybridisierung festgestellt werden. Trotz generell geringer genetischer Variabilität (*E. europaeus*: H_e = 0,019–0,02; P = 5,41; *E. concolor*: H_e = 0,000–0,02; P = 2,70–5,41), zeigten sich in beiden Arten signifikante regionale Genpool-Unterschiede. Der anhand des interspezifischen genetischen Distanzniveaus (NEI's (1978) D = 0.087–0.099) errechnete theoretische Speziationszeitraum der beiden Arten (vor 435 000–495 000 Jahren) entspricht der Hypothese einer pleistozänen Aufsplitterung eines ursprünglich einheitlichen europäischen Igel-Genpools in ein südöstliches und ein südwestliches Refugialgebiet und anschließender getrennter Evolution zu den beiden heutigen Igelarten.

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"Intervenors" in agonistic interactions amongst domesticated goats

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Abstract

Social behaviour was observed in individually marked goats in two herds. The goats from one herd (n = 98) were horned, those of the other herd (n = 83) were polled. By recording agonistic interactions within the herds, a dominance index was determined for each animal. In both herds, intervention took place. Intervention is defined as one animal pushing in between two fighters, and thus ending the fight.

More cases of intervention took place per individual animal amongst the horned goats than amongst the polled ones. Goats which intervened in fights on several occasions usually had a high dominance index. Members of the herd which were observed intervening only once had an average dominance index in both herds of almost 0.5. In some cases, goats very low in the rank order intervened a fight. Only rarely did the intervenors have a lower dominance index than the two fighters.

In 103 cases, the direct dominance relationship between a fighting animal and the intervenor was known. In 95 cases (92.2%), the intervenor was dominant to the herd member in this fight and in just eight cases (7.8%), it was subordinate. It could not be determined what advantage the intervenor gained from its activity. It is possible that, at least in certain cases, a particularly relationship existed between the intervenor and one of the fighters.

Key words: Goat, intervention, behaviour, domestication, rank order

Introduction

Many studies of the social behaviour of farm animals are concerned with the social rank order. Usually these are about the underlying factors which affect rank, the development of fights and other aggressive behaviour (i.e. threatening), as well as the effects of the dominance order on the individual animal. It is less frequently noted that there are also "friendly" interactions within groups of farm animals. An example of this is social grooming, eg. social licking amongst cattle (Sambraus 1969) and mutual nibbling amongst zebra (Andersen 1992).

One particular phenomenon of social behaviour is intervention. Intervention is described as an additional animal breaking up or disturbing an interaction between two or more of its conspecifics. Such interactions can be fights, sexual contact or even friendly behaviour (e. g. social grooming).

Intervention has been observed above all in primates (Seyfarth 1976; Kummer 1975; Silk 1982) and equines (Zeeb 1958; Klingel 1967; Feist and Mcullough 1976; Mattijs and Schilder 1990). But it also occurs in cattle (Sambraus 1969) and rats (Militzer 1995) and has even been described for fish (Walter and Trillmuch 1994).

This study aims at investigating situations, in which intervention takes place, in two large herds, one of horned and one of polled goats. Thus only small details of the term known in the broader sense as intervention, were recorded. The examination has been reduced to a large extent to the following areas: a) to determine the dominance index of the fighting animals and that of the intervening goat and b) to check what rank relationship those animals who were involved in the intervention, had to each other.

Material and methods

The observations were carried out on a farm in Bavaria. The total number of livestock was 800 goats, up to an age of twelve years. Originally kept were the breeds Coloured German Improved, White German Improved, Toggenburg, Saanen, and Anglo-Nubian goats. As the unit was concerned purely with milk yield, no value was put on retaining purebred stock. At the time of the observations, the animals were almost at the same stage of lactation. For the examination in hand, one group of horned and one of polled goats was chosen.

The group of horned goats contained 98 animals. This herd was put together about two weeks before the beginning of the observation period (end of February). The group of polled goats with 83 animals was formed more than two months before the beginning of the observation period. All animals were provided with plastic neck collars for individual identification.

The goats were kept in pens in an insulated, unheated building with ventilation through the eaves. The pens were 33.0 m long and 4.2 m wide (polled group), or 4.8 m wide (horned group). The floor space was therefore 1.7 m^2/animal in the polled group and 1.6 m^2/animal in the horned group.

Each pen was divided into halves, lengthwise; the lower resting area was straw bedded. Two steps led on to the feeding area 1 m higher up. The feeding area gave access to the feeding trough. Since the trough covered the whole length of the pen, all animals had access to it at the same time. The feeding of the two groups varied according to the different seasons at the time of the observations. For the horned goats (observation time was the end of February to the beginning of May), the feeding ration consisted of grass pellets, corn pellets, and hay ad lib. Feeding took place once a day, in the late morning. The polled group (observation time was the beginning of May to the end of June) received corn pellets as well as forage, twice a day, ad lib. (in the late morning and late afternoon).

Direct observations took place each week on three consecutive days. Between 07.15 hours and 18.00 hours there were four observation blocks with a total of eight hours. The observations were carried out from the long side of the pen. The results were written down by hand. All instances were recorded in which a goat interrupted an interaction between two others; in addition to this, behaviour displaying dominance, such as fights, the displacement of animals from the resting area, feeding or drinking troughs and avoidance or freezing of the threatened member of the herd.

At the close of the observation period, a dominance index was calculated for each goat. This was done by taking the number of animals over which an individual had shown itself to be dominant, and dividing it by the number of herd members for which a dominance relationship could be clarified. If, for example, 42 dominance relationships could be clarified for one animal and it proved itself to be superior to 27 herd members, then it received an index of 27 : 42 = 0.64. The rank index lies always between 0.0 and 1.0. Corrections as in Sambraus and Osterkorn (1974) or transformations to arcsin (Beilharz and Zeeb 1982) were not carried out.

Occasionally, when two herd members fought vigorously and lengthily with each other, a third one came and pushed in between the two fighters. This happened in a way, almost without exception, which was non-aggressive, very peaceful but forceful. With this, the opponents stopped the fight. Sometimes, however, several attempts at intervention were necessary, occasionally from several different intervenors in order to settle a conflict. Several attempts at intervention from one goat, on the one occasion, were however recorded as just one intervention. One particular goat made itself noticeable by getting up from distant resting places to put an end to fights.

For the horned goats, the length of the observation period was 25 days, for the polled goats, 20 days. The duration of the observation time each day was the same for both herds.

Results

One requirement for the interpretation of intervention was the recording of the social rank order of both herds. In principal, in a herd with n animals, n(n–1) : 2 rank relationships exist. In the herd with the 98 horned goats there were 4 753 different pairs. For the observation period, 3 083 situations demonstrating dominance behaviour were registered. From these, 1 980 cases of dominance relationships (41.7% of all possible relationships) could be clarified.

In the group of 83 polled goats, the total number of possible dominance relationships was 3 403. During the observation period, 2 304 cases demonstrating dominance-behaviour were seen. From there 1 489 dominance relationships (43.8% of all dominance relationships occurring in this herd) were clarified.

For the horned animals 66 interventions were observed during this period of time; for the polled goats, 15. In order to make the figures comparable, corrections had to be made to allow for the varying number of animals in the herds and the length of the observation time. When expressed per to 10 animals and 100 hours of observation, 3.37 interventions occurred amongst the horned goats, and 1.13 amongst the polled goats (Tab. 1).

Table 1. Details on „Intervention“ in one herd of horned and one of polled dairy goats

	herd	
	horned	polled
Number of animals	98	83
Days of observation	25	20
Total number of interventions	66	15
Number of interventions per 10 animals and 100 hours of observation	3.37	1.13
Average difference in dominance index between the two fighters	0.186	0.083
Average dominance index of the intervening goats	0.639	0.511
Number of interventions in the following dominance situation:		
– Intervenor has higher dominance index than both fighters	54	13
– Intervenor has higher dominance index than one of the two fighters	8	0
– Intervenor has lower dominance index than both fighters	4	2

The average difference between the dominance indices of the two opponents was 0.186 for the horned goats and 0.083 for the polled animals. It was, therefore, very small. In both herds, the intervenor usually had a higher dominance index than the two fighters. However, in the herd of horned animals there were intervenors whose dominance index lay somewhere between those of the two fighters. There were some animals both in the horned group as well as in the polled group, whose dominance index was less than those of the two goats involved in the aggressive situation.

The mean dominance index of the intervening goats lay on average at 0.639 (0.200–0.988) for the horned goats, for the polled goats at 0.511 (0.133–0.938). The intervenors were therefore not necessarily high ranking animals; amongst them were also low ranking animals. There were, however, amongst the horned as well as amongst the polled animals some goats, which intervened only once during the observation period. They had a mean dominance index of 0.539 (Tab. 2). On the other hand, within the herd of horned goats there were fourteen animals which intervened on several occasions (2–8 times). They had a mean dominance index of 0.800, i. e. were generally of high rank. Within the herd of polled goats, there was only one animal which intervened in a fight on several occasions (3 times). This goat also had a high dominance index (0.816).

Table 2. Dominance index of one-off and multiple interveners in the herds of horned and polled goats

	horned	polled
Number of intervenors, which intervened more than once	14	1
Frequency of the multiple interventions	2 to 8 times	3 times
Number of interventions through multiple intervenors	44	3
Adverage dominance index of multiple intervenors	0.800	0.816
Number of interventions by one-off intervenors	22	12
Average dominance index of one-off intervenors	0.539	0.486
Lowest dominance index of an Intervening goat	0.286	0.133

The dominance index reveals whether an intervenor has a high or a low position in the rank order. Because the social rank order is not linear, it does not reveal the dominance relationship existing between the intervenor and the two fighting animals. Hence, it was tested whether the intervenor was dominant or subordinate to the two fighters, as far as this was clear, during that particular clash.

In all, 81 cases of intervention were recorded (66 amongst the horned goats, 15 for the polled animals). As two fighting herd members were involved in each situation, the intervenors could have a fixed dominance relationship with 162 animals in total (Tab. 3). Because only just over 40% of all possible dominance relationships could be clarified in both herds, quite a lot of dominance relationships between fighters and intervenors remained unknown.

Table 3. Direct dominance relationships clarified between intervenors and fighters

	horned	polled	total
Number of interventions	66	15	81
Number of fighting animals taking part in the interventions	132	30	162
clarified dominance relationships between fighters and intervenors	87	16	103
from these the intervenor was dominant to ... fighters	80	15	95
from these the intervenor was subordinate to ... fighters	7	1	8
Interventions, in which the relationship of the intervenor to both fighters was clarified	31	5	36
Intervenor was dominant to both fighters	26	5	31
Intervenor was subordinate to one of the fighters	4	0	4
Intervenor was subordinate to both of the fighters	1	0	1

In total, the direct dominance relationship between one of the fighters and the intervenor could be clarified 103 times (63.6%). Out of these interactions the intervenor was dominant to one of the herd members taking part in the fight in 95 cases (92.2%), it was subordinate in only 8 cases (7.8%).

The dominance relationships of the intervenor to both fighters were known for 36 of the 81 intervened fights (44.4%). In 31 of these situations, the intervenor was dominant to both members of the herd involved in the fight (86.1%). In four cases, all within the herd of horned goats, the intervenor was subordinate to one of the fighters (11.1%), and, in one case, again within the horned group, the intervenor was subordinate to both fighters.

There were five goats who intervened in at least four fights during the observation period. All were horned, and therefore belonged to the herd with 98 individuals. One of these five goats was no. 14. She intervened five times. The herd member no. 37 took part in three of the fights. Goat no. 51 intervened in seven of the fights. The herd member no. 52 took part in three of these fights. Goat no. 54 was observed intervening four times. Once more the herd member no. 37 was involved here three times in a fight. Four fights were interrupted by no. 67, and in two of these no. 16 was involved. Only in the four fights interrupted by goat no. 84, did those involved change constantly.

Discussion

The term "intervention" means that one individual wants to influence the outcome of an interaction between group members (Mattijs and Schilder 1990). For example an intervenor may drive away rivals from females in heat (Sambraus 1973) or remove a certain group member, which is groomed by another, in order to take its place (Sambraus 1969).

Social behaviour is thought to be an expression on the controlling processes, so that an animal tries to bring an existing social situation in line with its idea of it. Wiepkema and van Hooff (1977) define this set point, which tells how a situation has to be, the norm value. It is possible that the purpose of the interventions we observed was to obtain a peaceful state. However, it is not clear what advantage the intervenor derives from such actions.

The observed interventions occur as well in wild ungulates, for example Scimitar-horned oryx (*Oryx dammah*) (Engel 1997) and Fringe-eared oryx (*Oryx gazella callotis*) (Feuerriegel 1997), the latter only referring to alpha males. The behaviour of interventions is not caused by the process of domestication and it is more likely to be seen in wild than in domesticated animals. Aggressive behaviour for example is shown in many domesticated species to a lesser degree than in the wild (Herre and Röhrs 1990).

Fighting animals are in danger of becoming injured. Necessarily their attention is fixed to each other and this leads to a decreased ability to look out for their predators and an increased risk to fall a prey. It is possible that the behaviour of interventions has a selective value for the purpose of species preservation.

But applying the above interpretation to a rather contrary behaviour leads to problems: Sometimes several herd members get aggressive when stimulated by two fighting animals, so that a so-called fighting-storm grows out of it. It is unlikely that big mammals like buffalo run a risk of being captured by predators while taking part in such a fighting-storm. However fighting-storms have also been observed in ibex (Walther 1960/61), a species that is indeed exposed to danger of being killed by predators.

Interventions seem to appear in wild animals mostly if the vehemence of a fight goes beyond a certain degree (Engel 1997; Feuerriegel 1997). Both groups of goats in this study intervened more if a fight exceeded a certain length of time.

Generally changes in behaviour resulting from domestication are a way of adapting to ecological conditions of housing (Herre and Röhrs 1990). Interventions happened much more often in the horned than in the polled group, even after adjusting for differing length of observation and number of animals. A possible explanation is that fights between horned individuals are more harmful than between polled goats. But it is not likely that these differences in the quantity of appearance of this behaviour are based genetically because all of the animals, the horned and the hornless, came out of one genpool.

It should be noted that the function of intervening was not only the right to one particular member of the herd. It must be emphasized, that there was an absolute alpha animal only in one of the two herds, in the polled group, which, measured on the scale of rank relationships already clarified, had a dominance index of 1.0 (Keil and Sambraus 1996). Amongst the horned group, goat no. 83 had the highest dominance index at 0.988.

Superior to her was goat no. 57 (three observations), but in turn eight members of the herd were superior to her, thus she had a dominance index of just 0.842 (Keil and Sambraus 1996). However, a highly ranked herd member has a special function during intervening. This still does not rule out the possibility that in isolated cases, members of the herd which have a position in the lower half of the rank order could also intervene in a fight.

In principal, animals with a low dominance index can also intervene in a fight. This conclusion becomes relative, however, when the actual dominance relationship of the intervenor to the fighters, is examined. Almost in all cases, the intervenor is dominant to both fighters. The function of the intervenor is obviously linked to a certain amount of authority. Thus, the exceptions are even more remarkable, when the intervenor is subordinate to one or both opponents.

Agonistic behaviour serves to re-establish a particular target value in social behaviour (Wiepkema and van Hoof 1977; Wiepkema et al. 1980). Matthijs and Schilder (1990) verify that this, in the same way, is valid for intervention. It is imaginable, that through intervention, a certain target value can also be re-established. In this study this question was not examined systematically. It is possible that the intervenor had a friendly relationship with one of the two fighters, as has been observed amongst cattle (Sambraus 1976). Goats in general demonstrate a very diverse type of social behaviour. Intervention, which has never before been described in this form occurring amongst other farm animals, confirms this.

Behaviour during intervention, and the course it takes, should be clearly distinguished from coalition, also observed amongst the animals. In this case, the goat approaching the two fighters clearly attacks one of the opponents and supports her actively, thus showing aggressive behaviour. A further form in which the animals react to fights amongst members of the herd, is the emergence of group fights. During these, more and more animals take part in a clash, the opponents changing frequently and new coalitions being built up, without there being a reccognisable outcome of the individual fights. Here the opposite of intervening behaviour is accomplished through the intervention of the animals, namely they succeed in unsettling a large part of the herd.

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Zusammenfassung

„Schlichter" bei sozialen Auseinandersetzungen von Hausziegen

Es wurden Beobachtungen zum Sozialverhalten von individuell gekennzeichneten Geißen in zwei Ziegenherden durchgeführt. Die Geißen der einen Herde (n = 98) waren gehörnt; die der anderen Herde (n = 83) waren hornlos. Für jedes Tier wurde aus zahlreichen Auseinandersetzungen mit Herdenmitgliedern ein Dominanzindex bestimmt. In beiden Herden kamen „Schlichtungen" vor. Das bedeutet, daß ein Tier sich zwischen zwei hartnäckig kämpfende Herdenmitglieder drängte und damit den Kampf beendete.

Bei den gehörnten Geißen kamen, bezogen auf das Einzeltier, mehr Schlichtungen vor als bei den hornlosen. Geißen, die mehrfach Kämpfe schlichteten, hatten gewöhnlich einen hohen Dominanzindex. Herdenmitglieder, die nur einmal als Schlichtende beobachtet wurden, hatten in beiden Herden einen durchschnittlichen Dominanzindex von nahezu 0,5. In einigen Fällen schlichteten sehr rangtiefe Geißen einen Kampf. Nur selten hatten Schlichtende einen niedrigeren Dominanzindex als beide Kämpfenden.

In 103 Fällen war das direkte Dominanzverhältnis zwischen einem kämpfenden Tier und der Schlichterin bekannt. In 95 Fällen (92,2%) war die Schlichterin diesem am Kampf teilnehmenden Herdenmitglied im Rang überlegen, nur in acht Fällen (7,8%) war sie ihm unterlegen. Es konnte nicht geklärt werden, welchen Vorteil die Schlichterin von ihrer Aktivität hat. Möglicherweise besteht zumindest in gewissen Fällen zwischen Schlichterin und einer der Kämpfenden ein besonders intensives Verhältnis.

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Comparative winter thermoregulation and body temperature in three sympatric *Apodemus* species (*A. alpicola, A. flavicollis,* and *A. sylvaticus*)

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Abstract

When living in sympatry with *Apodemus sylvaticus* and *A. flavicollis, A. alpicola* dominates numerically at higher altitudes. A more efficient winter thermal isolation or a higher winter thermogenic capacity procuring a physiological advantage could explain at least part of this domination. We therefore measured body temperature (Tb), oxygen consumption (VO_2), wet minimal thermal conductance (C) and non shivering thermogenesis (NST) at different ambient temperatures (Ta) on winter acclimated mice of the three species, and this for the first time in *A. alpicola*.

NST was high and C low in the three species. No significant difference could be noticed either in Tb between 5 and –10 °C, in VO_2 measurements at a Ta of –10 °C or in C. The NST measurements represent, respectively, 135.2% for *A. sylvaticus*, 142.8% for *A. flavicollis* and 140.5% for *A. alpicola* of the expected values, the values for *A. sylvaticus* being significantly lower than for the other two species. The basal metabolic rates (BMR) represent 169.4% for *A. sylvaticus*, 161.6% for *A. flavicollis* and 138.3% for *A. alpicola* of the expected values. Having removed the effect of body weight, the BMR value was significantly lower in *A. alpicola* than in *A. flavicollis*, but no difference could be noticed between *A. sylvaticus* and the other two species.

In conclusion, the three species of mice have very similar acclimated thermoregulatory characteristics, well adapted to cold ambient conditions. One discriminating and advantageous factor could be the lower basal metabolic rate measured in *A. alpicola* compared to the other two species.

Key words: *Apodemus*, rodents, thermoregulation, metabolism

Introduction

Mountain populations of small mammals are confronted with various limiting factors, the main ones being a short warm season, either for reproduction or constitution of winter reserves, and severe cold winter ambient temperatures. The temperatures in the Alps reach mean values between –1 and –8 °C during the winter period, with mean minimal values between –5 and –10 °C and extreme monthly mean minimal values of –11.5 °C beneath 2 000 m and –15 °C at 2 500 m (Swiss Meteorological Institute, data covering at least 20 years for the region presently investigated). These low temperatures require a high capacity for heat production, the main pathway for this production being NST, non shivering thermogenesis (Heldmaier et al. 1989). Seasonal acclimation of NST has now been well studied (Haim 1982; Haim and Yahav 1982; Cygan 1985; Feist and Feist 1986; Klaus et al. 1988; Heldmaier et al. 1981, 1989; Haim et al. 1995). This acclimation occurs

through a response to cold and/or to changes in photoperiod. Differences in NST level may be correlated to ecological speciation and adaptation to climatic conditions (Haim et al. 1984, 1993). For instance, rodents from desert areas with cold periods are characterized by high values of NST (Haim and Borut 1976; Haim and Fourie 1980). Wet thermal conductance is also a factor of importance in these conditions, even if the fur of small animals must remain short and light compared to larger forms (Scholander et al. 1950). The fur isolation properties change nevertheless between summer and winter (Hart 1956; Bolshakov 1984; review in Grodzinski 1985). Even at very low ambient temperatures, rodents may exploit actively atenuate climatic conditions by foraging under the snow cover and adjusting thermal isolation by adequate nest construction (Dufour 1972, 1978; review in Montgomery and Gurnell 1985). However, they must also be able to survive direct exposure to cold in spite of the high rate of heat loss due to their small size.

The Alpine mouse (*Apodemus alpicola*) with its distribution between 800 and 2 000 m is without doubt regularly exposed to severe climatic conditions. Described as an alpine subspecies of *A. flavicollis* by Heinrich (1952), its specific status was recognized by Storch and Lütt (1989) on morphological criteria. A biochemical confirmation was given by Vogel et al. (1991) and Filippucci (1992) for Italian, Austrian, and Swiss populations. The general distribution of this species was not known until recently for Austria (Spitzenberger and English 1996). Therefore, many biological data reported for "*A. flavicollis*" may in fact have been observed on *A. alpicola*.

As in Austria (Storch and Lütt 1989), *A. alpicola* may occur in the Swiss Alps forests in sympatry with *A. sylvaticus* and *A. flavicollis* (Vogel and Reutter, unpubl.), dominating numerically at higher altitudes. This domination may be explicited by many factors, either demographic, such as a possible higher natality for *A. alpicola*, or behavioral, such as a potential higher competition success for this species resulting in a lower mortality. Many of these factors are currently being investigated in the course of a PhD thesis by B. Reutter. According to Spitzenberger and English (1996), the fur of *A. alpicola* is particularly soft. This raises the question whether the Alpine mouse has a more efficient thermal isolation. In the present study we therefore investigated some energetic parameters under winter conditions. A lower thermal conductance or a higher thermogenic capacity may procure a physiological advantage, which could explain at least in part the domination of one of the three congeneric species.

Material and methods

Animals

All mice (24 individuals) were trapped during November 1996 in mountainous regions of Switzerland at altitudes ranging from 1 000 m to 1 400 m above sea level, thus accounting for a possible adaptation to altitude and harsh climates. Due to trapping hazards, the sex ratio of each species could not be controlled. The females were in no case pregnant. Depending on which experiment, the animals were held in captivity in outdoor conditions for 2 weeks to 5 months prior to measurements. They were housed in Macrolon® cages (type II: 40 × 25 × 15 cm), with a wire roofing, a sawdust floor and were fed ad libitum with apples, seeds, and water.

Experiments

Body temperature regulation (Tb)

5 *A. alpicola* (4 males, 1 female) and 5 *A. flavicollis* (5 females) were fitted with implanted thermodependant radio transmitters (Mini-Mitter X, Sunriver, Oregon, USA). Surgery was performed by a veterinary surgeon under total anaesthesia (Halothane, Halocarbon Laboratories, River Edge, U.S.A.). The signal sent by the transmitter was received by a loop antenna placed under the housing cage of the

subject. The period was measured by a high resolution timer-counter (Philips PM 6671). It was then recorded continuously on a recorder (W + W Elektronik AG., Basel, Switzerland) and was compared to a calibration curve established previously to the implantation.

Each measurement lasted 22 hours, 16 hours of which (2.00 pm to 5.00 am) were used in the analysis in order to avoid periods during which the animals were potentially disturbed or stressed. Four ambient temperatures were experienced (+5 °C, 0 °C, –5 °C, and –10 °C), the cages being placed in a cold chamber (±1 °C) (Frigorex, Villars-Ste-Croix, Switzerland or Weiss Technik AG., Kirchberg, Switzerland). The animals were fed ad libitum.

Hourly fluctuations of Tb over time, amplitude (as the difference between minimum and maximum body temperatures occurring at least 10 times during the 22 hours that the measurements lasted, Refinetti 1996) and maximum amplitude (as the maximum amplitude occurred during the 22 hours of measurement) were observed.

Oxygen consumption (VO_2)

Oxygen consumption of 5 *A. alpicola* (all males), 5 *A. flavicollis* (1 male, 4 females) and 5 *A. sylvaticus* (all males) was measured in an open circuit respirometer (Sparti and Genoud 1989). Five ambient temperatures (Ta) were experienced (5 °C, 10 °C, 15 °C, 20 °C, 30 °C). The animals were placed in a Plexiglas chamber (3.8 litres) in a thermostatized water bath (±0.1 °C). No food was offered.

The minimal values obtained at 30 °C are considered to be basal metabolic rates (BMR), within the thermoneutral zone (Cygan 1985; Haim et al. 1993). They are compared to the allometric equation $BMR = 3.45\ m^{-0.287}$ (McNab 1988; BMR in ml $O_2 \cdot g^{-1} \cdot h^{-1}$ and m in g).

Some additional data were obtained at a Ta of –10 °C with the 10 implanted individuals (5 *A. alpicola*, 5 *A. flavicollis*) used in the first experiment. The animals were housed in a larger metabolic chamber (15 litres) located in a cold chamber (Weiss Technik AG., Kirchberg, Switzerland).

The experiments lasted 4 hours. The resting metabolism at different temperatures was obtained over a stable minimum period of 5 minutes at least.

Thermal conductance (C)

The simultaneous measurements of body temperature and metabolism obtained at the lowest tested ambient temperature (–10 °C) allowed a precise calculation of the wet thermal conductance of *A. flavicollis* and *A. alpicola*, following the formula $C = VO_2/(Tb–Ta)$ (McNab 1980). C is considered minimal at this temperature. A second set of measurements of Tb was made on the other set of non-implanted individuals of the three species at the end of each measurement of oxygen consumption between 5 and 30 °C. Tb was this time measured by means of a rectal probe (Bat-12, Sensortek, Bailey, USA). C was calculated following the same formula and the minimal values for each individual chosen. These results were then compared to the allometric equation $C = 0.76\ m^{-0.426}$ (Bradley and Deavers 1980; C in ml $O_2 \cdot g^{-1} \cdot h^{-1}\,°C^{-1}$ and m in g).

Non shivering thermogenesis (NST)

NST measurements of the same individuals used for the oxygen consumption experiments were made following the methods of Heldmaier (1971) and Sparti (1992). The amount of noradrenalin (NA) injected was calculated following the formula given by Heldmaier (1971), plus an amount of 0.004 mg NA after preliminary control experiments, in order to have a maximum response. The NA (Arterenol, Hoechst) was injected intraperitoneally and the animal placed immediately in the respirometer. Oxygen consumption was measured following the procedure explained above, at a Ta of 15 °C in order to avoid a possible overheating of the animal.

Two successive measurements were realized for each individual in order to control the validity of the data. The first were made at the end of March, the animals being kept under a natural photoperiod and temperature. The second session took place one month later, after acclimation to a controlled short photoperiod (8 L : 16 D) and low regulated temperature.

The results were compared to the expected values according to $NST = 30\ m^{-0.454}$ (Heldmaier 1971; NST in ml $O_2 \cdot g^{-1} \cdot h^{-1}$ and m in g).

Results

Body temperature (Tb)

In order to ensure independence of the data, measurements of body temperature at one hour intervals over a period of 16 hours were used (Fig. 1). Body temperature decreased slightly with ambient temperature in *A. alpicola*, but not in *A. flavicollis* (Fig. 2).

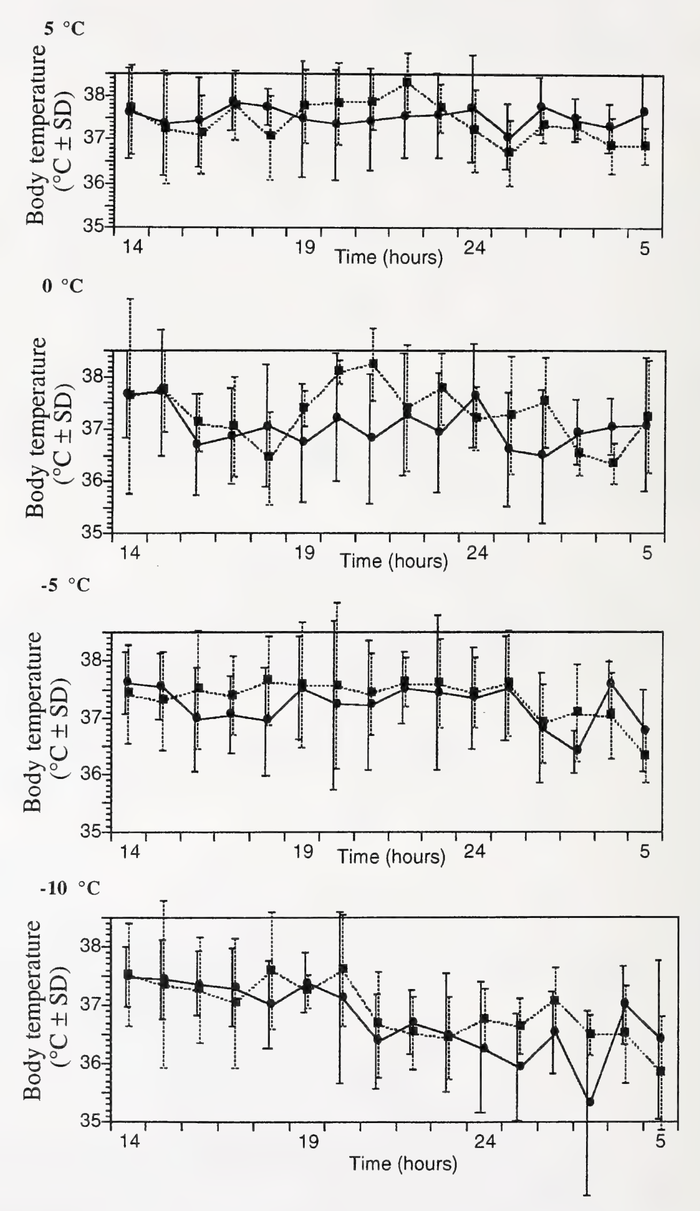


Fig. 1. Daily fluctuations in body temperature (°C ± SD) at four ambient temperatures (N = 5 for *A. flavicollis* ---■--- and N = 5 for *A. alpicola* —●—).

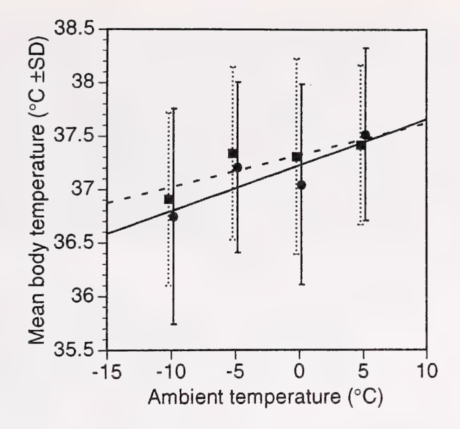


Fig. 2. Mean body temperatures (±SD) over a period of 16 hours at four ambient temperatures (N = 5 for *A. flavicollis* - - -■- - - and N = 5 for *A. alpicola* —●—). Regression lines are: Tb = 37.32 + 0.03 Ta ($r^2 = 0.19$; p = 0.058) for *A. flavicollis*, and Tb = 37.24 + 0.04 Ta ($r^2 = 0.30$; $p < 0.05$) for *A. alpicola*.

Repeated-measurements ANOVAs applied to each ambient temperature showed no statistical differences either between the level of body temperatures over 16 hours (between 2.00 pm and 5.00 am) between *A. alpicola* and *A. flavicollis* or in the fluctuations of body temperatures over time (all interactions Time × Species: NS). Tb was independent of the hour of the day at all ambient temperatures except –10 °C ($F_{(15/120)} = 3.83$, $P < 0.0001$), the lower body temperatures being recorded during the night, at the end of the measurement.

The largest amplitudes and extreme amplitudes were determined with the data of all ambient temperatures pooled for every individual (Tab. 1). No statistical difference could be observed between the two species (Student t-test: NS). The especially large standard deviation (±2.44) of the extreme amplitude in *A. flavicollis* is due to an individual who experienced a short torpor bout during one experience at –10 °C.

Table 1. Mean amplitude (±SD) and extreme amplitude (±SD) of Tb for *A. flavicollis* and *A. alpicola*. All Ta are pooled.

	N	Amplitude (°C)	Extreme amplitude (°C)
A. flavicollis	5	4.61 ± 1.05	6.26 ± 2.44
A. alpicola	5	5.88 ± 1.52	6.64 ± 1.14

Oxygen consumption (VO_2)

Oxygen consumption was measured at 6 different ambient temperatures (Fig. 3). The results at Ta = –10 °C are treated separately because these measurements were made on a different set of individuals. Between 5 and 30 °C, oxygen consumption increased with decreasing ambient temperature (Tab. 2). The lines intercept the ambient temperature axis at, respectively, 49 °C for *A. sylvaticus*, 46 °C for *A. flavicollis*, and 48 °C for *A. alpicola*. These temperatures are higher than the observed body temperatures. This shows clearly that the wet thermal conductance is not independent of ambient temperature.

Having removed the influence of body weight, the basal metabolic rate (BMR) values are significantly different for the three species (ANCOVA, $F_{(2/12)} = 7.85$, $p < 0.01$) and significantly lower for *A. alpicola* than *A. flavicollis.* (Scheffé Post Hoc Test: *A. alp.* – *A. flav.*: p = 0.01). No significant difference is observed between *A. sylvaticus* and the other two species. The measured oxygen consumptions represent for *A. sylvaticus* 169.4%, for *A. flavicollis* 161.6% and for *A. alpicola* 138.3% of the expected values.

At the other extreme of the range of measurements, the comparison of the metabolic rates at –10 °C between *A. flavicollis* and *A. alpicola* shows no significant differences between both species (ANCOVA, $F_{(1/7)} = 0.87$, NS).

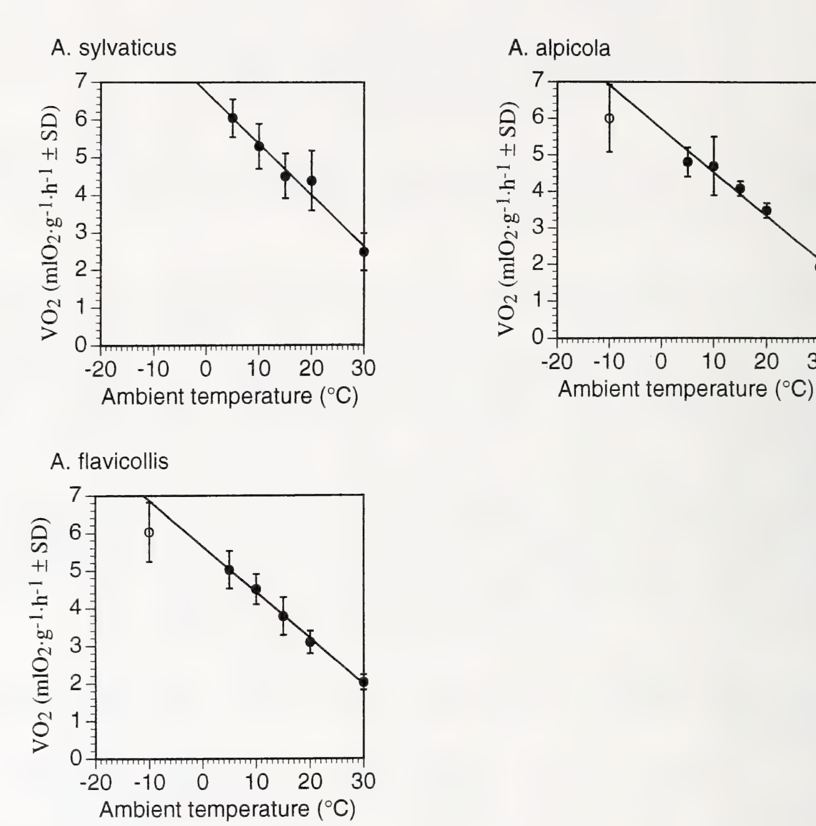


Fig. 3. Mean relative oxygen consumption (VO_2, ml $O_2 \cdot g^{-1} \cdot h^{-1} \pm$ SD) at different ambient temperatures. The equations of the regression from 5 to 30 °C are given in table 2. (N = 5 individuals for each species. A different set of individuals was used at Ta = –10 °C).

Table 2. Relation between ambient temperature (Ta, °C), body weight (m, g) and oxygen consumption (VO_2, $mlO_2 \cdot h^{-1}$) between 5 and 30 °C.

	N	Regression	r^2	p
A. sylvaticus	5	$LogVO_2 = 1.87 + 0.32$ Log m-0.02 Ta	0.915	$p < 0.0001$
A. flavicollis	5	$LogVO_2 = 1.76 + 0.36$ Log m-0.02 Ta	0.943	$p < 0.0001$
A. alpicola	5	$LogVO_2 = 2.06 + 0.16$ Log m-0.02 Ta	0.959	$p < 0.0001$

Thermal conductance (C)

Two methods were used to assess Tb: implantation and rectal probe (Tab. 3). A significant difference exists between the two values of C for *A. alpicola* (ANCOVA, $F_{(1/7)} = 8.41$, $p < 0.05$) and for *A. flavicollis* (ANCOVA, $F_{(1/7)} = 8.56$, $p < 0.05$). The relative values are inferior to the expected values in all cases. No significant statistical difference was observed either between the two species measured by implantation (ANCOVA, $F_{(1/7)} = 0.000$, NS) or between the three species measured by rectal probe (ANCOVA, $F_{(2/11)} = 0.99$, NS).

Table 3. Mean absolute (C ± SD, $mlO_2 \cdot h^{-1} \cdot °C^{-1}$) and relative (Crel ± SD, $mlO_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$) thermal conductance measured for *A. flavicollis*, *A. alpicola*, and *A. sylvaticus* with two sets of individuals and two methods used to measure Tb: implantation or rectal probe; m is the body mass (g) and *Δ*% is the difference between Crel and the expected values.

		N	C	Crel	m	Δ%
A. flavicollis	Implant.	5	3.36 ± 0.44	0.13 ± 0.02	28.81 ± 7.31	71.6
A. alpicola	Implant.	5	3.46 ± 0.31	0.14 ± 0.02	25.03 ± 3.57	72.6
A. flavicollis	R. probe	5	4.93 ± 0.39	0.15 ± 0.02	33.26 ± 3.66	87.8
A. alpicola	R. probe	5	4.57 ± 0.50	0.15 ± 0.01	31.08 ± 3.25	85.3
A. sylvaticus	R. probe	5	4.60 ± 0.41	0.18 ± 0.02	25.56 ± 2.03	94.2

Non shivering thermogenesis (NST)

All individuals reached a high oxygen consumption within minutes following the NA injection (Fig. 4). The consumption remained at a maximum level for a variable length of time, between 5 and 30 minutes. The metabolic rate then diminished progressively.

No significant statistical difference was observed between the two series of measurements for each species taken separately (ANCOVA, NS). The consumption of *A. sylvaticus* was significantly lower than the other two species in the first NST measurements (ANCOVA, $F_{(2/10)} = 7.97$, $p < 0.01$, Scheffé Post Hoc Test: *A. sylv.* – *A. flav.*: $p < 0.05$, *A. sylv.* – *A. alp.*: $p < 0.05$) but no difference remained after the second series of measurements (ANCOVA, $F_{(2/10)} = 0.66$, NS).

The first series of NST measurements represent, respectively, 135.2% for *A. sylvaticus*, 142.8% for *A. flavicollis* and 140.5% for *A. alpicola* of the expected values.

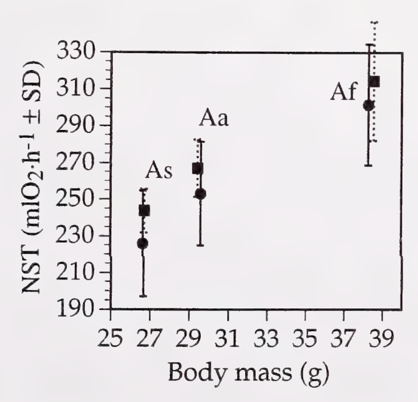


Fig. 4. Maximum mean NST consumptions (ml $O_2 \cdot g^{-1} \cdot h^{-1}$ ± SD) and body mass (g) for the 1st (- - -■- - -) and 2nd (—●—) series of measurements. (N = 5 for *A. sylvaticus* (As) and *A. flavicollis* (Af) and N = 4 for *A. alpicola* (Aa)).

Discussion

Oxygen consumption (VO_2) and body temperature (Tb) at various ambient temperatures (Ta), as well as non shivering thermogenesis (NST) values and minimal wet thermal conductance (C), were measured for the first time in *Apodemus alpicola*. These same measurements were also realized for the first time on a taxonomically controlled sample of *A. flavicollis*. All the experiments were made under winter conditions, the animals being kept outdoors under natural temperatures and photoperiod, and all animals having been caught at high altitudes. Furthermore, the individuals were subjected to cold conditions during the measurements without any kind of external structure procuring an isolated warmer microclimate, such as the one they should be expected to use in nature: padded nests, tunnels, passages under the snow, etc. The data obtained should therefore give a good indication of the physiological capacities these species, as well as *A. sylvaticus*, possess to survive winter in their mountainous habitat.

All three species are obviously well adapted to cold conditions. The winter NST values found are high (about 140%). This result is close to the data in the literature. HAIM et al. (1995) found a value equal to 117% of the allometry for *A. sylvaticus* at an acclimation Ta of 24 °C and a short photoperiod. HELDMAIER et al. (1989) found a value of 139% of the allometry for cold acclimated *A. flavicollis* under a short photoperiod. The differences between these values and ours are probably due to the samples, but also to the methods used. The temperatures and photoperiod during acclimation, as well as the length of the acclimation period, or the differences in Ta during the experiences may cause these discrepancies.

Wet thermal conductance values are low (between 72 and 94% depending on the method and the species) compared to the allometry of BRADLEY and DEAVERS (1980). Our values are similar to the data found in the literature for *A. sylvaticus*. HAIM et al. (1995) found $0.186 \pm 0.021\ mlO_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$ ($m = 24.7 \pm 2.9$ g), i. e. 95.9% of the expected value. Literature data concerning the other species are missing. However, we consider that the results obtained employing the method of implantation are reliable. Oxygen consumption and Tb were measured simultaneously, the delay due to the respirometry system being negligible and thus allowing a precise calculation of C, and no handling of the individuals was necessary. Ambient temperature was also lower during the measurement, so that C was more likely to be at its minimal value. The data for *A. sylvaticus*, obtained using the rectal probe method, are therefore perhaps slightly overestimated.

NST and C are both essential adaptations allowing the presence of these species all year round in this type of habitat. *A. flavicollis* and *A. alpicola* were both capable of regulating their Tb at ambient temperatures between +5 °C and –10 °C. The mean Tb *A. alpicola* maintained was slightly influenced by Ta, but the slope of this relation is weak. *A. flavicollis* lost 0.5 °C and *A. alpicola* lost 0.7 °C between the mean body temperatures at 5 and –10 °C. Oxygen consumptions at –10 °C were high, but still well below the NST consumptions measured. CYGAN (1985) measured the VO_2 sum of *A. flavicollis* in an $He\text{-}O_2$ atmosphere (thus at cooling conditions corresponding to –30 °C), finding $13.6 \pm 1.6\ mlO_2 \cdot g^{-1} \cdot h^{-1}$ ($m = 31.1 \pm 5.7$ g). This is also well above the oxygen consumptions obtained, in the present study, at –10 °C. No limitation seems then to arise from an eventual aerobic maximum reached at this temperature. It was, however, only at –10 °C that the time of the day had an influence on the measurements, Tb being minimum at the end of the experience. Low temperatures seem then to be a limiting factor at least when the animals are exposed during long periods, although it is difficult to explain the causes. The temperatures we tested do not, however, affect the survival of animals fed ad libitum, even when –10 °C represents an extreme in the temperatures that a small mammal can experience for long periods.

These results are not surprising. All three species are regularly found at high altitude

habitats subjected to cold winters. *A. sylvaticus* is the most wide spread. It is present at all altitudes and has been captured in Switzerland up to 2 200 m. Data concerning *A. flavicollis* are more problematic: some or many of the observations made between 1 400 and 2 000 m should potentially be attributed to *A. alpicola*. An extreme observation has been made at 2 450 m above sea level, but incertainty remains on the species determination between *A. flavicollis* and *A. alpicola* (Yoccoz 1992). This third species has been found in Austria up to a height of 1 900 m (Spitzenberger and Englisch 1996). In conclusion, one of the corollaries of altitude, cold, seems to be a limitation in the home range, but the three species seem well armed against it. It is, however, difficult to have an exact idea of the microclimates that the small mammals must face in winter. They may be relatively well sheltered under the snow cover, under rocks, in crevasses or deep in the ground, and this even more so when they possess a well-isolated nest. What happens when they must leave these places? For instance, low temperatures might be present without snow covering the ground. More precise data on these microclimates are required.

Having established that all three species are relatively well adapted to mountainous conditions, what can be said about interspecific differences? No difference can be observed between *A. alpicola* and *A. flavicollis* either for NST values, C values, VO_2 at –10 °C or Tb (level, evolution, and amplitude) at any Ta. Less numerous comparisons have been made with *A. sylvaticus*, but NST values were significantly lower in this species than in the other two in the first series of measurements. This, added to the highest C value compared to the allometry, could reflect a different adaptation of this species. This result must, however, be taken with caution as no difference remained between species after the second series of measurements. An effective difference in the capacity to produce or use brown adipose tissue (BAT) may exist, but it must be slight, as attested by the almost similar percentages obtained when compared to expected values of NST.

A more important feature may be the basal rate of metabolism (BMR). *A. alpicola* has the lowest BMR of the three species. It is statistically different to *A. flavicollis* and is the smallest when compared to expected values. Literature data give even higher winter BMR values for *A. flavicollis* than ours, e. g. 175% (m = 35 g; Klaus et al. 1988), 207% (m = 29 g; Heldmaier et al. 1989) or 238% (m = 31.1 g; Cygan 1985) of the allometry. A lower rate may be an adaptation to habitats susceptible to experience food or water shortages in the case of arid or semi-arid species (Haim 1987). Food may also be more difficult to find and collect in the Alps during winter but an individual should find itself at a Ta situated in or very close to the thermoneutral zone to be able to benefit from this advantage on species of almost similar body weight and C. It should be noted that a low BMR is not directly linked to a low thermogenic capacity. At a specific level, BMR, maximum metabolism in the cold and NST are independent (Sparti 1992). A high BMR is therefore not a direct advantage in cold conditions.

The few purely physiological differences between species pointed out are not of course sufficient to explain the predominance of one species over the others. Many other factors should be taken into account. Other physiological data are still missing, in particular in the case of *A. alpicola*. Many species experience a loss in body weight during winter (Dehnel 1949), as in the case with *Clethrionomys glareolus* (Klaus et al. 1988). *A. sylvaticus* seems to maintain a constant body weight throughout the year (Klaus et al. 1988), while *A. flavicollis* is heavier during winter (Cygan 1985 ; Klaus et al. 1988). A body weight loss occurring in *A. alpicola* would perhaps represent an advantage if the food supply is precarious. The maximum rate of energy assimilation may also be a limitation. Koteja (1995) measured this maximum rate in *A. flavicollis* and found a value much smaller than the short-term maximum consumption measured previously (Cygan 1985), thus indicating a limiting factor. This should also be investigated in *A. alpicola*. Torpor is another important means of saving energy or resources. Torpor bouts have been observed in several temperate Muridae, in particular in *A. sylvaticus* (Morris 1968; Walton and Andrews 1981)

and *A. flavicollis* (CYGAN 1985). One *A. flavicollis* individual experienced three torpor bouts during two measurements we made at –10 °C. The torpors lasted 160 ± 34 min. Tb fell to 28.51 ± 0.25 °C and oxygen consumption to 6.4 ± 0.3 $mlO_2 \cdot g^{-1} \cdot h^{-1}$. Investigations should be made concerning the capacity of *A. alpicola* to experience torpors, both in the laboratory and in the field. Behavior can also have an essential impact on thermoregulation. Nest sharing, for instance, has been shown to reduce thermoregulatory costs. Such a behavior has been measured, for instance, in *A. flavicollis* (FEDYK 1971) and *A. agrarius* (TERTIL 1972). If this sharing occurs in nature in *A. alpicola*, a difference in social habits between species may be of importance. Intra- or interspecific competition may also be a means of ensuring the possession of the best nesting sites or resources. *A. flavicollis* is the heaviest species and was found superior in interspecific encounters with *A. sylvaticus* (CIHAKOVA and FRYNTA 1996). MONTGOMERY (1980) stated that interspecific spatial segregation between these two species is maintained by *A. sylvaticus* avoiding the competitively superior *A. flavicollis*. The body weight difference is smaller between *A. alpicola* and the other two species, thus more or less aggression could make the difference.

In conclusion, the three species of mice tested in the present study have very similar acclimated thermoregulatory characteristics, well adapted to cold ambient conditions. One discriminating and advantageous factor could be the lower basal metabolic rate measured in *A. alpicola* compared to the other two species. Many other physiological, behavioral, and populational factors remain to be measured.

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Zusammenfassung

Vergleichende Winterthermoregulation und Körpertemperatur bei drei sympatrischen Apodemus-Arten (A. alpicola, A. flavicollis und A. sylvaticus)

Bei sympatrischem Vorkommen der drei Waldmaus-Arten *Apodemus alpicola*, *A. sylvaticus* und *A. flavicollis* in höheren Lagen dominiert *A. alpicola* zahlenmäßig. Eine effizientere thermische Isolation im Winter oder eine erhöhte thermogenetische Kapazität, die einen physiologischen Vorteil mit sich bringt, könnten eine Erklärung für diese Dominanz sein. Hierfür wurden an winterangepaßten Waldmäusen der drei Arten die Körpertemperatur (Tb), der Sauerstoffverbrauch (VO_2), die Wärmedurchgangszahl (C), und die zitterfreie Wärmebildung (NST) bei verschiedenen Umgebungstemperaturen (Ta) gemessen. Für *A. alpicola* wurden diese Messungen erstmals durchgeführt.

Für die zitterfreie Wärmebildung fand man bei sämtlichen drei Arten hohe, für die Wärmedurchgangszahl tiefe Werte. Weder aus den Messungen der Körpertemperaturen bei Umgebungstemperaturen zwischen 5 und –10 °C, des Sauerstoffverbrauches bei einer Umgebungstemperatur von –10 °C noch der Wärmedurchgangszahlen resultierten signifikante Unterschiede. Die Messungen der zitterfreien Wärmebildung ergaben für *A. sylvaticus* 135.2%, für *A. flavicollis* 142.8% und für *A. alpicola* 140.5% des erwarteten Wertes, wobei die Zahlen von *A. sylvaticus* signifikant tiefer liegen als diejenigen der beiden anderen Arten. Der Grundumsatz (BMR) ergab für *A. sylvaticus* 169.4%, für *A. flavicollis* 161.6% und für *A. alpicola* 138.3% des erwarteten Wertes. Vernachlässigt man das Körpergewicht, liegt der BMR-Wert von *A. alpicola* signifikant tiefer als derjenige von *A. flavicollis*. Keinen Unterschied fand man hingegen zwischen *A. sylvaticus* und den beiden anderen Arten.

Abschließend sei erwähnt, dass die drei Waldmaus-Arten ähnliche thermoregulatorische Eigenschaften besitzen, die eine gute Anpassung an kalte Umgebungstemperaturen zulassen. Einzig der tiefere BMR-Wert von *A. alpicola* könnte sich, gegenüber den beiden anderen Arten, als vorteilhaft erweisen.

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Geographic structure, gene flow, and maintenance of melanism in *Ctenomys rionegrensis* (Rodentia: Octodontidae)

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Abstract

Ctenomys rionegrensis has three coat color morphs (melanic, agouti, and dark-backed) within its total distribution of 50 × 60 km area of Uruguay. The presence of two populations fixed for the melanic form is remarkable because this coat color contrasts markedly with the surrounding substrate. Starch gel electrophoresis was used to analyze variation in 20 allozyme loci assayed in 100 individuals from seven populations of *C. rionegrensis* to test the hypothesis that melanism was fixed by genetic drift in small, isolated populations. Seven loci were monomorphic (95% criterion) and no alleles correlated exclusively with a particular coat color. Average heterozygosity was H = 0.038 (range 0.022–0.058). Using pairwise comparisons of all populations, the mean number of migrants ($\hat{M}$) was 6.342 for all pairs except those involving the population at Los Arrayanes (agouti), for which the average value was 1.532. Our results indicate that gene flow in *C. rionegrensis* is sufficiently high to prevent fixation of alternative alleles exclusively by drift. The absence of a pattern of genetic variation due to isolation by distance suggests that the current distribution resulted from a recent range expansion.

Key words: Tuco-tucos, geographical structure, gene flow, genetic drift, melanism

Introduction

There are at least three possibilities that explain patterns of differentiation when populations differ in gene frequencies: 1) populations have been molded by natural selection, with the selective agents spatially structured; 2) populations show the effects of genetic drift, and 3) patterns may result from intermixing of different stocks (i. e., gene flow). These possibilities are not mutually exclusive and may operate in combination to produce the observed patterns of geographic variation.

There is full consensus concerning the feasibility of natural selection to produce geographic variation (Mayr 1963). The effects of genetic drift in randomly changing allele frequencies are also clear. Drift may fix or eliminate alleles from populations and in the process lead to divergence among populations (e. g., Gallardo and Köhler 1994). Finally, gene flow has long been considered as a homogenizing evolutionary force, although gene flow could promote divergence by dispersing new genes and gene combinations throughout a species' range. The role that gene flow plays depends both on the importance of other evolutionary forces and on the geographic distribution of the species (Slatkin 1987).

Ctenomys rionegrensis Langguth and Abella, 1970 is one of the three Uruguayan species of the diverse genus *Ctenomys* (tuco-tucos). The species occurs in a restricted area of

about 3 000 km^2 in southwest Uruguay in the Department of Río Negro. Despite its restricted distribution, three color morphs are known: melanic, agouti, and dark-backed. Melanic individuals of this species are entirely and uniformly black, whereas agouti specimens may exhibit slightly dark dorsal areas on the head (Langguth and Abella 1970 a). Dark-backed individuals are characterized by a wide mid-dorsal band of dark grey-brown hair, which runs from the snout to the base of the tail (Altuna et al. 1985). Some populations are monomorphic for the melanic morph, others for the agouti morph, while others are comprised exclusively of dark-backed individuals. Populations that are polymorphic with respect to pelage are known. In these, melanic and agouti or agouti and dark-backed individuals coexist.

The chromatic differentiation of *C. rionegrensis* is interesting because it occurs in a restricted geographic area. This differentiation is not correlated with different soil colors, as was suggested for *C. torquatus* by Freitas and Lessa (1984) and demonstrated for populations of pocket gophers (Geomyidae) (Patton and Smith 1990), nor with variation in other environmental characteristics. All *C. rionegrensis* populations examined live in sandy meadows, which are uniformly light colored with no obvious variation in soil or vegetation.

The genetic structure of fossorial rodents, such as *Ctenomys*, has been thought to reflect their low vagility, and therefore, low levels of gene flow. Further, the supposed small size of demes has been thought to make them more susceptible to the random effects of genetic drift in fixing or eliminating alleles (Reig 1970; Reig et al. 1990; White 1978). Since selection-based explanations of color variation have not been supported for some *C. rionegrensis* populations, fixation of melanism may be due to genetic drift (Altuna et al. 1985; Langguth and Abella 1970 b). This hypothesis predicts 1) reduction in genetic variation within melanic populations and 2) low levels of gene flow among the populations, such that genetic drift would cause divergence among populations. The first prediction would pertain only if the populations fixed for the melanic forms passed through a bottleneck (Templeton 1981; see also Barton and Charlesworth 1984). The second prediction is more general and indicates that genetic drift can be an effective agent of local differentiation (Slatkin 1987; Wright 1931; cfr. Wright 1969).

In an attempt to distinguish these forces, extensive field work has been aimed at describing the distribution of *C. rionegrensis* and the spatial frequency of pelage variants. We have begun to characterize genetic variation across populations in an effort to discriminate among the various hypotheses concerning the origin and present distribution of the melanic form. Specifically, we 1) define levels of intrapopulation genetic variation with nuclear markers (allozymes); 2) establish the levels and patterns of intraspecific microgeographic differentiation; and 3) estimate gene flow between the populations.

Material and methods

One hundred specimens of *Ctenomys rionegrensis* from seven localities were collected in 1993 and 1994 and examined (Fig. 1). Specimens from Las Cañas and Nuevo Berlín were exclusively melanic, whereas all those from Mafalda and Tres Bocas were dark-backed. Polymorphic populations included El Abrojal (4 melanic, 16 agouti) and La Guarida (8 dark-backed, 4 agouti). All specimens from Los Arrayanes were agouti; however, 3 out of 18 specimens collected in Los Arrayanes in 1983 were melanic. Those individuals were not included in this study because tissue samples were not preserved.

Individuals were captured with Gopher Ready Set traps and prepared as voucher museum specimens now archived in the collection of the Laboratorio de Evolución, Facultad de Ciencias, Montevideo. Tissues (heart, liver, kidney) were extracted immediately after sacrificing the animal and stored at –80 °C. Protein electrophoresis was performed on liver homogenates with horizontal starch gels. Electromorphs were stained using standard techniques (Tab. 1) (Selander et al. 1971; Harris and Hopkinson 1976).

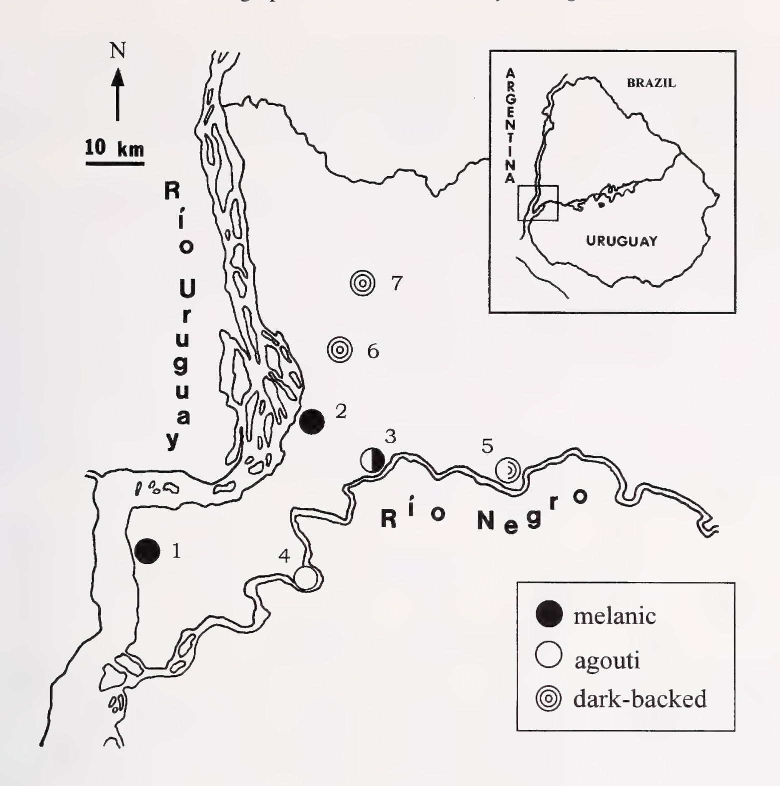


Fig. 1. Map of the studied zone. In brackets the sample sizes of the 7 populations of *Ctenomys rionegrensis.* 1) Las Cañas (16); 2) Nuevo Berlín (10); 3) El Abrojal (20); 4) Los Arrayanes (18); 5) La Guarida (12); 6) Mafalda (15); and 7) Tres bocas (9).

Table 1. Proteins, loci abbreviations, Enzyme Commission number, and electrophoretic conditions used in the study of populational differentiation in *Ctenomys rionegresis.* A = acid citrate buffer, pH 6.1/6.0, 76 mA/5 h; B = tris-citrate buffer, pH 8.0/8.0, 115 mA/5 h.

Protein	Locus abbreviation	Enzyme Commission number	Electrophoretic conditions
Adenylate kinase	ADK	(2.7.4.3)	A
Alcohol dehydrogenase	ADH	(1.1.1.1)	B
Aspartate aminotransferase	AAT1, AAT2	(2.6.1.1)	A
Glutamate dehydrogenase	GDH	(1.4.1.3)	B
Glycerol 3-phosphate dehydrogenase	α-GPD	(1.1.1.8)	B
Isocitrate dehydrogenase	ICD1, ICD2	(1.1.1.42)	A
Lactate dehydrogenase	LDH1, LDH2	(1.1.1.27)	B
Malate dehydrogenase	MDH1, MDH2	(1.1.1.37)	A
Malic enzyme	ME	(1.1.1.40)	B
Phosphoglucomutase	PGM1	(2.7.5.1)	B
Phosphogluconate dehydrogenase	6-PGD	(1.1.1.44)	A
Superoxide dismutase	SOD1, SOD2	(1.15.1.1)	A
General protein	GP1, GP2, GP3		A

Differences in the mobility of electromorphs were assumed to have a genetic basis and to follow rules of simple Mendelian inheritance. Side by side comparisons were carried out to confirm the identity of electromorphs across gels. Alphabetic designations were assigned to the different electromorphs of each presumptive locus, with a representing the fastest migrating electromorph in both anodal and cathodal systems.

BIOSYS-1 (Swofford and Selander 1981) was used to assess the average number of alleles per locus, (A), the percentage of polymorphic loci, (P), average heterozygosity per individual per observed population, (H), Wright's F-statistics and Nei's (1978) and Rogers' (1972) genetic distances. Option 5 of GENEPOP 1.2 (Raymond and Rousset 1995) was used to test for statistically significant differentiation in allele frequencies between pairs of populations. The matrix of Rogers' unbiased distances was used to construct a Wagner tree in BIOSYS-1 (Swofford and Selander 1981), and to carry out a multidimensional scaling with the program STATISTICA (1995). Gene flow was estimated by two methods. First, the effective number of migrants Nm was estimated using the private alleles method (Slatkin 1985) and option 4 of the program GENEPOP 1.2 (Raymond and Rousset 1995). Second, a method based on Fst estimated the levels of gene flow between pairs of populations, with the program DIST (Slatkin 1993) using the formula $\hat{M} = [(1/F_{ST})-1]/4$ where θ of Weir and Cockerham (1984) was used as an estimator of Fst. Estimates of gene flow, $\hat{M}$, for each pairwise comparison were then plotted against geographic distances between populations following Slatkin (1993).

Results

Variation within populations

Genetic variation was assayed at 20 presumptive loci, which code for 12 enzymes and 3 general proteins (Tab. 2). Under the criterion that the most common allele had a frequency not higher than 95%, seven loci were monomorphic whereas this value was four under the criterion of 99%. All other loci had two or three alleles that varied in frequency among populations (Tab. 2). No alleles were exclusive to a pelage morph but some were unique to populations. ICD-2b, ME a, SOD-1a, and GP-3c were exclusive to the Los Arrayanes population, but the latter three were at frequencies of less than 0.05. GP-3a and SOD-2b were only found in La Guarida, but the latter was at less than 0.05. The proportion of polymorphic loci under the 95% criterion varied from 0.1 in Las Cañas to 0.4 in Nuevo Berlin, and the average value was 0.25.

Table 2. Allelic frequencies, mean number of alleles per locus (A), percentage of loci polymorphic (P), mean heterozygosity (H), and sample sizes for populations of *Ctenomys rionegrensis*. Loci abbreviations are defined in table 1.

Population		1 Las Cañas	2 Nuevo Berlín	3 El Abrojal	4 Los Arrayanes	5 La Guarida	6 Mafalda	7 Tres Bocas
	n	16	10	20	18	12	15	9
Locus	Allele							
ADH	a	0.688	0.500	0.600	0.861	0.667	0.833	0.833
	b	0.312	0.500	0.400	0.139	0.333	0.167	0.167
ADK	a		0.050		0.028	0.042		
	b	1.000	0.950	1.000	0.972	0.958	1.000	1.000
AAT-1	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT-2	a						0.167	0.111
	b	0.969	1.000	0.950	0.750	1.000	0.833	0.889
	c	0.031		0.050	0.250			

Table 2. (Continued)

Population		1 Las Cañas	2 Nuevo Berlín	3 El Abrojal	4 Los Arrayanes	5 La Guarida	6 Mafalda	7 Tres Bocas
	n	16	10	20	18	12	15	9
GDH	a						0.033	
	b	0.906	0.900	0.900	0.917	0.833	0.934	1.000
	c	0.094	0.100	0.100	0.830	0.167	0.033	
GPD	a	0.031		0.025	0.028	0.083		
	b	0.969	1.000	0.975	0.972	0.917	1.000	0.944
	c							0.056
ICD-1	a			0.050			0.067	
	b	1.000	1.000	0.950	0.972	1.000	0.933	1.000
	c				0.028			
ICD-2	a	1.000	1.000	1.000	0.556	1.000	1.000	1.000
	b				0.444			
LDH-1	a	0.031						
	b	0.969	0.950	0.925	1.000	0.917	0.967	1.000
	c		0.050	0.075		0.083	0.033	
LDH-2	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH-1	a				0.028			
	b	1.000	0.950	1.000	0.972	1.000	1.000	1.000
	c		0.050					
MDH-2	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ME	a				0.028			
	b	1.000	1.000	1.000	0.972	1.000	1.000	1.000
PGM	a					0.083		
	b	1.000	0.950	1.000	1.000	0.917	1.000	1.000
	c		0.050					
6-PGD	a			0.025	0.028	0.042	0.033	
	b	1.000	0.950	0.975	0.944	0.958	0.967	1.000
	c		0.050		0.028			
SOD-1	a				0.028			
	b	1.000	1.000	1.000	0.972	1.000	1.000	1.000
SOD-2	a	1.000	1.000	1.000	1.000	0.958	1.000	1.000
	b					0.042		
GP-1	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GP-2	a		0.050		0.028			
	b	0.969	0.950	0.925	0.972	0.917	1.000	1.000
	c	0.031		0.075		0.083		
GP-3	a					0.083		
	b	1.000	1.000	1.000	0.972	0.917	1.000	1.000
	c				0.028			
A		1.30	1.40	1.40	1.70	1.50	1.35	1.15
P (95%)		10.00	40.00	30.00	25.00	35.00	20.00	15.00
H		0.028	0.050	0.040	0.058	0.038	0.033	0.022
(±1 SE)		(0.013)	(0.015)	(0.016)	(0.017)	(0.014)	(0.018)	(0.013)

The average heterozygosity per individual per population (direct count) ranged from 0.022 in Tres Bocas to 0.058 in Los Arrayanes, and the average was 0.038. These values are similar to those observed in other underground rodents: 0.038 (Nevo et al. 1990), in particular those found in *Geomys bursarius*: 0.039 (Bohlin and Zimmermann 1982), *Ctenomys maulinus:* 0.040 (Gallardo and Köhler 1992), *C. lewisi*: 0.032 (Cook and Yates 1994), and *C. australis*: 0.030 (Apfelbaum et al. 1991). In contrast, the values of *C. rionegrensis* are higher than those of *C. argentinus*: 0.000 (Sage et al. 1986); *C. frater*: 0.012, *C. steinbachi*: 0.009 (Cook and Yates 1994), and lower than those in the *C. mendocinus*: 0.065 group (Sage et al. 1986), *C. porteousi*: 0.081 (Apfelbaum et al. 1991), *C. flamarioni*: 0.175, *C. torquatus*: 0.110, *C. minutus*: 0.114, and *C.* sp: 0.141 (Moreira et al. 1991) and *Thomomys bottae*: 0.088 (Patton and Smith 1990). The value of these comparisons is relative, because the enzymatic systems used in this study are different from cited cases, except Cook and Yates (1994). This difference can bias observed heterozygosities (see Gillespie and Kojima 1968). For example, there are clear cases in which including or excluding esterase loci from the analysis drastically affects the outcome (Apfelbaum et al. 1991; Ortells and Barrantes 1994).

Wright's (1969) Fis statistics show that five loci (ADH, GDH, GPD, PGM, and GP-2) have significant positive departures from Hardy-Weinberg equilibrium in an overall analysis across all populations. Similarly, Fis values were significantly greater than zero in two populations (Los Arrayanes and La Guarida) in analyses across all loci. In all these cases, Fis values were positive, indicating a deficit of heterozygotes (Tab. 3).

Table 3. Statistically significant ($P < .05$) Fis values. Globally, two populations (Los Arrayanes and La Guarida) have a significant deviation from the Hardy-Weinberg equilibrium across all loci ($P = .0079$ and $P = .0014$).

Locus	Los Arrayanes	La Guarida	Mafalda	Across populations
ADH	.779	.651	.774	.556
GDH		1.000		.493
GPD		1.000		.337
PGM		1.000		.596
GP-2		1.000	1.000	.465
ICD-1	.575			
GOT-2				

Table 4. Estimates of the genetic distances between 7 *Ctenomys rionegrensis* populations based on allelic frequencies of 20 loci. The lower triangular matrix is Rogers' (1972) distances; while the upper triangular matrix is Nei's (1978) distances.

Population	1	2	3	4	5	6	7
1 Las Cañas		0.000	0.000	0.013	0.000	0.001	0.001
2 Nuevo Berlín	0.027		0.000	0.019	0.000	0.006	0.005
3 El Abrojal	0.015	0.025		0.015	0.000	0.003	0.003
4 Los Arrayanes	0.056	0.071	0.064		0.015	0.011	0.011
5 La Guarida	0.030	0.036	0.029	0.077		0.003	0.002
6 Mafalda	0.027	0.044	0.030	0.052	0.050		0.000
7 Tres Bocas	0.022	0.045	0.035	0.053	0.049	0.015	

Geographic variation

In some comparisons, genetic distance between pairs of populations with the same pelage color is higher than between populations with different pelages (Tab. 4). Three main groups are distinguished (Fig. 2): the Los Arrayanes population, the populations Mafalda and Tres Bocas, and the populations of Las Cañas, El Abrojal, Nuevo Berlin, and La Guarida. Los Arrayanes is the most divergent population. Pairwise comparisons of populations (Option 5 of GENEPOP, Raymond and Rousset 1995) show no significant differences in allele frequencies between populations within each group, but significant differences in comparisons of populations from different groups (results not shown). Multidimensional scaling of genetic distances (Lessa 1990) reveals neither a clinal pattern, nor any other type of simple correlation between the geographic and genetic distances (Fig. 3).

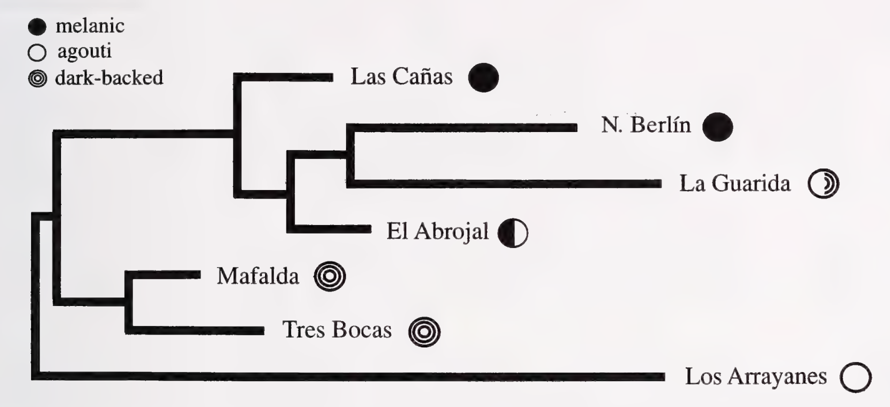


Fig. 2. Wagner tree of genetic relationships among seven populations of *Ctenomys rionegrensis* based on Roger's genetic distances (Tab. 4). The tree is rooted at midpoint of greatest patristic distance.

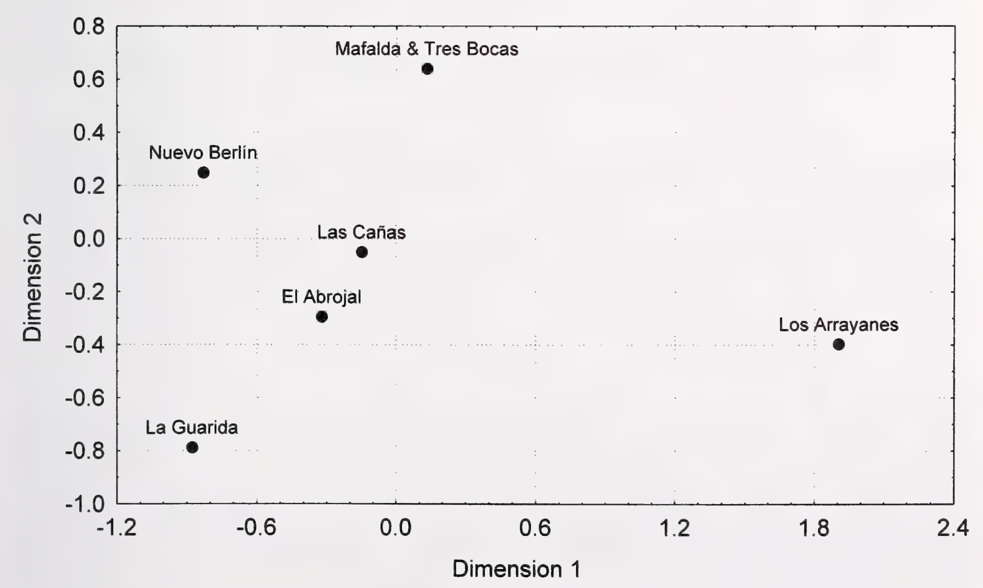


Fig. 3. Multidimensional scaling of genetic distances in two dimensions for the 7 *C. rionegrensis* populations, based on Rogers' genetic distances (Tab. 4).

The average value of F_{ST} for all loci is 0.091, indicating that only 9.1% of the total variation is due to population subdivision. This reveals geographic subdivision on the same order as that found in *C. australis*: 0.128 (APFELBAUM et al. 1991), though lower than that estimated for *C. maulinus*: 0.330 (GALLARDO and KÖHLER 1992), and *Thomomys bottae*: 0.258 (PATTON and SMITH 1990).

Gene flow

The private alleles method estimated the number of migrants per generation considering all populations to be 1.713. SLATKIN's (1993) method generally showed no pattern of isolation by distance between the different populations (Fig. 4). Specifically, values of gene flow were high between the two melanic populations and between them and all other populations except Los Arrayanes. Values were lowest between Los Arrayanes and all others (average value of $\hat{M} = 1.532$). The average value of gene flow between all populations excluding Los Arrayanes was $\hat{M} = 6.342$. Figure 4 shows the relationship between geographic distance and gene flow for all pairs of populations yielding positive estimates of $\hat{M}$. Negative estimates cannot be log-transformed and are therefore missing (Fig. 4). Those values indicate extremely low genetic differentiation (SLATKIN 1993).

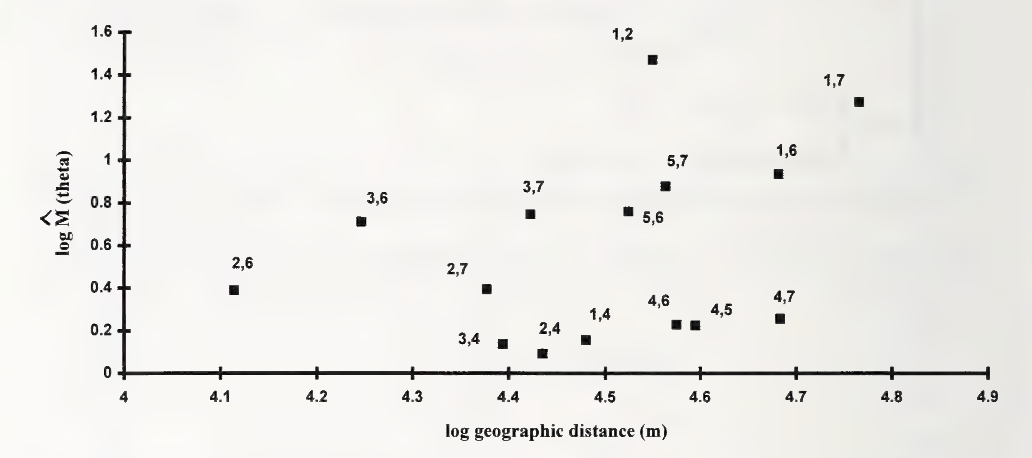


Fig. 4. Levels of gene flow ($\hat{M}$) between pairs of populations plotted against the geographic distances between them, in kilometers. The values of gene flow were estimated according to SLATKIN (1993) with the formula $\hat{M} = [(1/F_{ST})-1]/4$, using θ of WEIR and COCKERHAM (1984) as an estimator of F_{ST}. The estimations of $\hat{M}$ for 6 pairs of populations do not appear because the corresponding F_{ST} values are zero or not significantly different from zero (see text).

Discussion

Drift is considered to have a fundamental role in genetic and karyotypic evolution of subterranean rodents (PATTON and YANG 1977; SAGE et al. 1986). Presumed low vagility and the discontinuity of the subterranean ecotype are thought to have fragmented populations into isolated demes. Thus, a low level of gene flow exists between populations and the effects of drift and differentiation could be pronounced. With this classical image of the evolutionary dynamics of the subterranean rodents, it was thought that the fixation of melanism in some populations of *C. rionegrensis* occurred by genetic drift (ALTUNA et al. 1985; LANGGUTH and ABELLA 1970b). This hypothesis, in turn, may be

specified in two ways: 1) invoking a bottleneck in the history of an ancestral population in which melanism became fixed; and 2) proposing generally low levels of gene flow among populations.

Our estimates of heterozygosity and polymorphism are similar in melanic and non-melanic populations. More generally, they are comparable to those found in other subterranean rodents (NEVO et al. 1990). These data suggest no reason for invoking a bottleneck that would have facilitated the fixation of melanism. The expectation in that scenario would be one of reduced genetic variability, as observed for example in Chilean populations of tuco-tucos that have experienced such events (GALLARDO and KÖHLER 1994; but see BARTON and CHARLESWORTH 1984).

Our estimated levels of gene flow between the melanic and other populations, and generally within the species, are rather high, with the exception of Los Arrayanes, which maintains significantly lower levels of exchange and is the most genetically dissimilar population. High levels of gene flow were also found among populations of *C. australis* separated by distances between 58 and 112 km and this allowed only mild local differentiation (average value of $F_{ST} = 0.128$ APFELBAUM et al. 1991).

The values of gene flow between the populations are expressed as the number of migrants per generation, Nm and pairwise values are estimated by $\hat{M}$. An average of at least one individual per generation exchanged between two populations will prevent alternative neutral alleles at the same locus from being fixed by genetic drift (WRIGHT 1931; cfr, WRIGHT 1969). This is independent of population size. The measures of genetic exchange in this study are indirect estimates of historial, rather than current levels of gene flow among populations (SLATKIN 1987). They measure levels from some point in the species' evolutionary past, which coupled with other evolutionary forces, have shaped current patterns of genetic variation.

It seems unlikely that current levels of gene flow are as high as suggested by the observed values and here we note that the barriers currently restricting gene flow could not have existed in the past. This apparent contradiction between direct and indirect methods of estimating gene flow probably means that the species has undergone large-scale demographic changes in the recent past (SLATKIN 1987). The absence of isolation by distance and in *C. rionegrensis* coupled with high values of $\hat{M}$ may indicate that these populations colonized their present ranges recently (SLATKIN 1993). These populations are beginning to differentiate under the effects of isolation, but insufficient time has elapsed to permit accumulation of substantial genetic differences. The case for a recent expansion is reinforced by the low levels of population subdivision observed. Recent colonization of new areas, as postulated here, was also assumed for different karyomorphs of the "Corrientes group" of *Ctenomys*, to explain high estimates of gene flow ($\hat{M}$) (ORTELLS and BARRANTES 1994).

Taken as a whole, our results suggest that the hypothesis of random fixation of melanism (i.e., due to drift) is unlikely. Our results are compatible with the more complex evolutionary dynamics of demographic instability. A history of recent expansion could have maintained the populations of *C. rionegrensis* far from an equilibrium of isolation by distance, in which the furthest populations would be the most differentiated ones, and in which small isolated demes are susceptible to differentiation via drift of the founder effect type of Mayr (BEATTY 1992). Cycles of expansion and contraction may have been caused partially by Pleistocene marine transgressions, which are known to have reached the zone of the present distribution of *C. rionegrensis* (ALONSO 1978; SPRECHMANN 1978). Flooding is locally known to affect some populations. In this context, the melanic populations may not be demographically independent of other populations. Gene flow may be a significant evolutionary process if movements of individuals or entire populations spread genes and combinations of genes throughout the range of a species. This situation may have produced the current geographic distribution of characters in *C. rionegrensis*. With

regards to gene flow in subterranean rodents, Patton and collaborators (Patton and Feder 1981; Patton and Smith 1990), have shown that it can vary dramatically in different circumstances. For instance, high levels of "connectedness" by gene flow are quite likely in densely populated areas, as illustrated by *C. rionegrensis.* High levels of gene flow do not lower the importance of drift; however, the fixation of melanism by drift alone is unlikely. Natural (including sexual) selection may affect pelage color, but we are far from understanding in what manner. A similar case of chromatic polymorphism, maintained by natural selection in spite of high levels of gene flow, has recently been reported in garter snake populations (Lawson and King 1996).

Combining direct sequencing and restriction enzyme analysis, we have generated preliminary data on levels of mitochondrial DNA variation in *C. rionegrensis.* Those data involved 140 individuals from nine populations including those analyzed here, Eight substitutions, defining three haplotypes, were detected. One of the haplotypes is widely distributed, while the other two have more restricted distributions. Mitochondrial DNA diversity is very low and not strongly structured, which reinforces the idea that differentiation is probably recent in populations of *C. rionegrensis.*

Finally, it is important to point out that the field work has provided valuable information about the demography of the species. For instance, chromatic polymorphisms are frequent and sometimes transient. For example, in Los Arrayanes, there was a ratio of agouti to melanic individuals in 1983 of 5 to 1. Specimens collected ten years later were exclusively agouti in spite of intensive sampling. The polymorphic populations may have originated through persistence of an ancestral polymorphism or through recent gene flow between previously isolated populations. These alternatives would indicate, respectively, that these are zones of primary or secondary contact. Preliminary estimations (made by multiplying the number of individuals captured within a quadrat by the total area occupied by the population) suggest that the populations consist of several thousand individuals. Also, we have recently found polymorphic populations with different combinations of pelage colors (e. g., melanic and agouti at La Tabaré, and all three morphs in sympatry at Portones de Chaparei). All these observations suggest that populations are more dynamic than previously thought and gene flow has had an important role in population structure. Future studies with more variable molecular markers will allow us to test hypotheses about the fixation of melanism by natural selection, and to generate a more complete picture of the evolutionary dynamics of this species.

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Zusammenfassung

Geographische Struktur, Gen-Fluß und Erhaltung von Melanismus bei Ctenomys rionegrensis (Rodentia: Octodontidae)

In seinem gesamten uruguayischen 60×50 km großen Verbreitungsgebiet weist *Ctenomys rionegrensis* drei Fellfärburgen auf: melanistisch, agouti und „dorsal" dunkel. Die Anwesenheit von zwei Populationen für die melanistische Form ist erwähnenswert, da diese Färbung stark mit der Umgebung im Kon-

trast steht. Um die Hypothese zu testen, daß Melanismus in kleinen Populationen mit geringem oder keinem Gen-Fluß von benachbarten Populationen durch genetische Drift festgelegt ist, wurde Stärke-Gel Elektrophorese angewandt. Die Variation in 20 allozymen Loci von 100 Individuen aus 7 Populationen wurde geprüft. Sieben Loci waren monomorphisch (95%) und keines der Allele korreliert allein mit einer bestimmten Fellfärburg. Die durchschnittliche Heterozygotie war H = 0.038 (Variabilität 0.022–0.058). Der paarweise Vergleich aller Populationen ergab einen $\hat{M}$ Durchschnittswert von 6.342 für alle Paare, mit Ausnahme der Population von Los Arrayanes (agouti), dessen Durchschnittswert 1.532 erreichte. Unsere Ergebnisse zeigen, daß der Gen-Fluß bei *C. rionegrensis* ausreichend hoch ist, um der Fixierung von alternativen Allelen ausschließlich vorzubeugen. Der Mangel an einem von der Distanz abhängigen genetischen Variationmusters deutet an, daß die heutige Verbreitung das Ergebnis einer jüngeren Raumerweiterung sein könnte.

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Reproductive characteristics and growth in the eusocial Zambian Common mole-rat (*Cryptomys* sp., Bathyergidae)

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Abstract

A large data set on reproduction, growth, and juvenile mortality in captive eusocial Zambian common mole-rats (*Cryptomys* sp.) has been statistically evaluated. The gestation length was 98 days (range 84–112 days). The mean litter size was 2.4 (SD = 0.9; range 1–5; n = 102). Larger litters (4 and 5) were generally rare but rather frequent in two multiparous females. The mean neonate weight was 7.9 g (ranging from 5.7 g to 10.7 g) and was negatively correlated with the litter size. The neonate and suckling mortality was about 34% and was higher in males; so that the sex ratio (male/female) of sucklings eight weeks after birth was 0.7 : 1 (n = 159). The growth within the first 20 weeks of age was linear (at a rate of about 0.27 g/day) and independent of gender, litter size or family size. The growth constants calculated according to the Gompertz equation were very low (K = 0.006; n = 17). The prediction of the aridity hypothesis of eusociality in mole-rats that the first litters born to pairs should grow faster than litters born to established families was not supported by the evaluation of a larger sample size. Pregnant and at the same time lactating females restricted their investment to embryos and fetuses but not to sucklings. The growth and developmental rate in Zambian mole-rats seems to be a conservative rather than a plastic trait. We may assume (or at least we cannot exclude) that the slow developmental rate is one of the causes rather than a consequence of (eu)sociality.

Key words: Eusociality, mole-rat, growth, reproduction, Bathyergidae

Introduction

Two genera of the African bathyergid mole-rat, the naked mole-rat (*Heterocephalus*) and Gray's mole-rats (*Cryptomys*) are unique among the subterranean rodents in particular and among mammals in general. These mole-rats live in colonies whose structure can be denoted as eusocial: the reproduction is monopolized by a single female and her mate(s), whereas most of their offspring remain within the parental family throughout their lives and do not reproduce (JARVIS 1981; BURDA 1990; BURDA and KAWALIKA 1993; JARVIS and BENNETT 1993; JARVIS et al. 1994).

Two alternative hypotheses address the ultimate functions of this unique social system. A cooperative (or aridity) hypothesis (e.g., JARVIS and BENNETT 1991; JARVIS et al. 1994; LOVEGROVE 1991) relates sociality in mole-rats to small body size, semi-aridity of the habitat (rainfall less than 350 mm) and prevalent feeding on large but widely spaced geophytes. The scenario assumes that cooperative foraging evolved in semi-arid areas where the risk of dispersal and failure to find enough food is high. The second hypothesis of phylogenetic and developmental constraints (BURDA 1990; BURDA and KAWALIKA 1993) argues that sociality of *Heterocephalus* and *Cryptomys* is a conservative trait reflecting sys-

tematic relationships of bathyergids to hystricognath rodents. According to this hypothesis the eusociality in mole-rats is merely a special case of a cooperative breeding system based on monogamy and helpers. The monogamy and helpers are considered to be necessary for successful reproduction since the female mole-rat alone may not be able to rear her offspring competently (BURDA 1990; BURDA and KAWALIKA 1993). The point of the dispute between both hypotheses is whether the reason for origin and current function of eusociality are identical.

In any case, even the proponents of the aridity hypothesis speak of eusociality as of a cooperative breeding (and not e. g., a cooperative foraging) system (cf. JARVIS et al. 1994). Hence it is not surprising that considerable attention has been paid to the study of reproductive biology in mole-rats by both research groups. The relatively long gestation periods and slow growth found concordantly in all the social bathyergid mole-rats have been, however, interpreted differently – either as a consequence of sociality (e. g., BENNETT et al. 1991) or as one of its causes (BURDA 1990). BENNETT et al. (1991) and BENNETT and AGUILAR (1995) pointed out even relatively slight differences in growth rates and litter sizes among different species of *Cryptomys* from different habitats and they looked for adaptive meaning for these differences. However, their data were based on the examination of only very few cases and calculated for incomplete growth periods. Such an analysis can be connected with substantial mathematical errors (BEGALL 1997).

To assess the variation in reproductive parameters (and thus the justification of interpretations based on interspecific comparisons of small samples) we analysed our extensive breeding data in a Zambian species of common *Cryptomys*.

Material and methods

Animals

Gray's common mole-rats (*Cryptomys* sp., karyotype 2 n = 68) originating from the Lusaka area, Zambia, were kept in captivity (at the University of Frankfurt am Main and the University of Essen) since 1986. We denoted these animals *C. hottentotus* in our earlier studies. The Lusaka population is, however, specifically distinct from typical *C. hottentotus* from South Africa and should be considered a new species, not yet formally named (FILIPPUCCI et al. 1994).

The animals were kept in pairs and families in plastic or glass cages on horticultural peat. They were fed ad libitum by carrots, potatoes, apples, lettuce, and cereals. For further details on housing conditions, see BURDA (1989, 1990). All individuals were weighed at least once a week with an accuracy of 0.01 g.

For the size of the sample examined, see the particular results and tables.

Mathematical analysis

The growth parameters were described using the Gompertz equation:

$$W(t) = A \cdot e^{-e^{-K(t-I)}}$$

where $W(t)$ = weight (g) at time t (days); A = asymptotic value (g); K = growth constant (days^{-1}); I = age at the inflection point (days). All three growth parameters were estimated using the Levenberg-Marquardt-iteration.

The Gompertz model was employed only in those individuals for which the complete data set (from birth to accomplished growth) was available. Maximum growth rates (growth at the inflection point I) were determined by multiplying the growth constant K by $A \cdot e^{-1}$. The slope of the regression line was estimated for each individual separately in order to describe the individual growth rate in the juvenile period of the first 20 weeks after birth.

Table 1. The size of the sample examined for reproductive characteristics in particular species of *Cryptomys* mole-rats.

species	mothers	litters	pups	reference
C. damarensis	5	6	20	BENNETT and JARVIS (1988) BENNETT et al. (1991)
C. h. hottentotus	2	2	6	BENNETT (1989) BENNETT et al. (1991)
C. darlingi	2	7	12	BENNETT et al. (1994)
C. mechowi	2	5	8	BENNETT et al. (1994)
C. mechowi	2	2	3	BURDA and KAWALIKA (1993)
C. sp. (2n = 68)	7	21	45	BURDA (1989, 1990)
C. sp. (2n = 68)	18	102	241	present study

Results

Neonates: gestation, litter size, sex ratio and body weight

The previous findings (BURDA 1989, 1990) concerning the length of gestation (= 98 days; range 84–112 days) were confirmed. The average litter size was 2.36 (SD = 0.94; range 1–5; n = 102). Litters with twins comprised 40%, litters with triplets 33%, those with single pups 18% of all litters (Tab. 2). The larger litters were rather rare and were delivered by only few mothers. One female produced four litters of four, another female gave birth to one litter of four and three litters of five. It should be noted that the first litters of these females were, however, smaller and larger litters occurred only after at least two years of successful reproduction.

Table 2. Numbers, neonate weight, and mortality rate in dependence on the litter size in captive Zambian common mole-rats.

litter size	number of litters	weight of neonates mean (SD, n)	mortality rate (%)
1	18	8.6 (1.3, 13)	16.7
2	41	8.1 (1.2, 47)	39.0
3	34	7.7 (0.9, 48)	40.2
4	6	7.4 (0.9, 14)	16.7
5	3	7.1 (0.7, 10)	13.3

The sex (male/female) ratio of neonates was 0.85 : 1 (98 males : 115 females). The sex in additional 28 newborn pups could not be determined, mostly because these pups have died or been killed and eaten by their respective mothers before being sexed.

The average body weight of neonates was 7.90 g (n = 132). Males were slightly heavier (7.99 g, SD = 1.16, n = 59) than females (7.82 g; SD = 1.12; n = 73), the difference being, however, not significant (t-test; $P = 0.406$). The weight ranged between 5.7 g and 10.7 g and was negatively correlated with the litter size (Pearson; $r = -0.35$; $P < 0.001$) (Tab. 2, Fig. 1).

Mortality of neonates and sucklings

While the mortality in grown-up mole-rats is negligible, it was rather high among neonates and sucklings. Zambian common mole-rats are suckled for at least eight weeks (mostly longer, cf., BURDA 1989, 1990), therefore the age of eight weeks was set as a limit for this analysis.

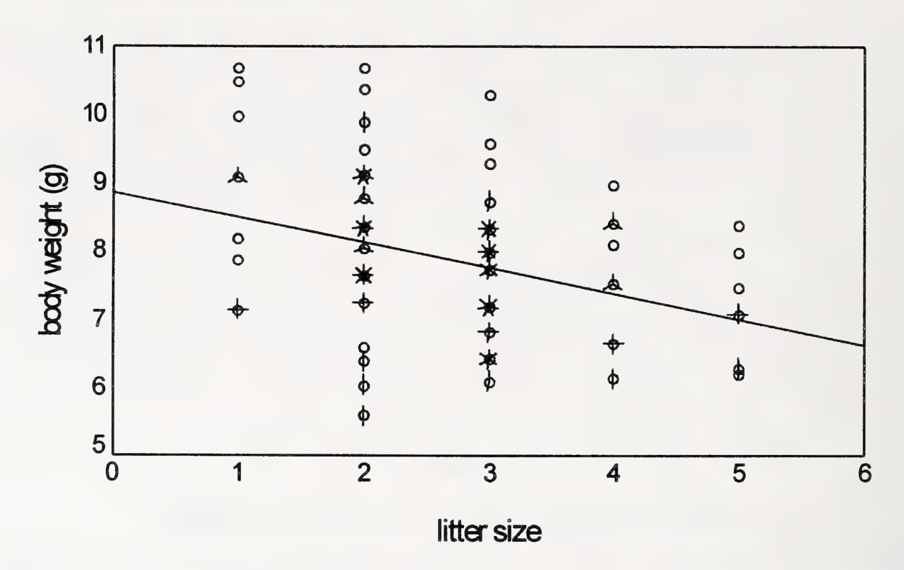


Fig. 1. Correlation between the weight of neonates and the litter size in Zambian common mole-rats.

Table 3. Numbers of survived and died pups (within first eight weeks of age) in captive Zambian common mole-rats.

litter size	survived		died			total
	males	females	males	females	unidentif.	
1	4	11	2	1	0	18
2	23	27	12	9	11	82
3	26	35	14	10	17	102
4	8	12	3	1	0	24
5	6	7	0	2	0	15
total	67	92	31	23	28	241

The mortality rate of neonates and sucklings within the first eight weeks of age was 34% (including pups of unidentified sex). The mortality rate was significantly higher in males (32%) than in females (20%) ($\chi^2 = 6.92$; 5% level) (Tab. 3).

Mortality rate could be related to the neonate weight: 32.6% of a total of 49 pups with a neonate weight under or equal to 7.0 g died within the first eight weeks of age, while only 15.7% of a total of 83 pups with a neonate weight more than 7 g did not survive ($\chi^2 = 5.19$; 5% level). There was no apparent correlation between the survival (mortality) rate and the litter size (cf., Tab. 2): mortality rates were very low in large litters (4 and 5). Since these large litters were delivered only by a few mothers, the mortality rate seems to depend on the mother rather than on a litter size. There was a positive correlation between the normal (i.e., non-pregnant) body weight of the mother and the survival rate of the pups (Pearson; $r = 0.5$; $P < 0.001$) (Fig. 2). We also found an indication of a positive effect of helpers (or a larger group size) on the survival of pups. However, the correlation was weak ($r = 0.3$; $P = 0.038$).

Pups conceived in a postpartum estrus and/or during lactation and born before or when the elder siblings (pups of the previous litter) reached a critical weight of 35 g (weaning weight, cf., BURDA 1989) had significantly (t-test; $P = 0.038$) lower birth weights

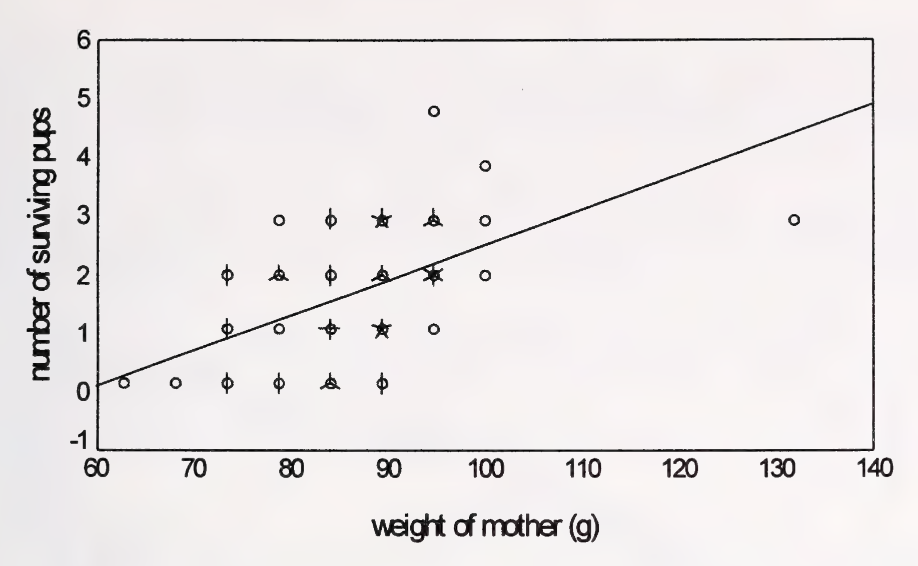


Fig. 2. Correlation between the number of survived pups and the weight of the non-pregnant mother.

(mean 7.59 g; SD = 0.98; n = 21) than pups born after their elder pups had been weaned (mean 8.16 g; SD = 1.16; n = 54). Consequently, there was a higher probability of survival in pups born after their elder siblings were fully weaned ($\chi^2 = 5.87$; $P = 0.0154$). This effect is obvious when the critical weaning weight but not the age of the elder siblings is considered (Tab. 4).

Table 4. Correlation of mortality of pups with critical parameters (weight of 35 g and age of 20 weeks) of elder siblings at time of birth in Zambian common mole-rats.

	weight of elder siblings		age of elder siblings	
	<35 g	≥35 g	<20 weeks	≥20 weeks
survived pups	22	61	42	40
died pups	19	20	21	19
total	41	81	63	59

Growth

Gompertz modell

The growth data of grown-up animals aged at least 75 weeks (females) or 90 weeks (males) were analysed using the Gompertz equation (Tab. 4). The asymptotic values (A) and the maximum growth rates ($K \cdot A \cdot e^{-1}$) were significantly higher for males than for females (t-test; $P < 0.001$ and $P < 0.01$) although the growth constants K did not differ significantly (t-test; P=0.783).

Factors affecting growth

Gender

During the first 18 to 20 weeks after birth there was practically no weight difference between males and females and the growth was almost linear (Fig. 3). The growth equations for this juvenile phase: $y = 1.83x + 7.6$ (females) and $y = 1.99x + 6.7$ (males) gave the following growth rates: 0.26 g/day (females) and 0.28 g/day (males).

Litter size

Since there were not enough data for larger litter sizes, only the litters with single, twins, and triplets were assessed. There was no obvious effect of the litter size upon the growth rate: $y_1 = 2.1\,x + 8.7$; $y_2 = 2.2\,x + 7.2$; $y_3 = 2.1 + 6.0$ (Fig. 4).

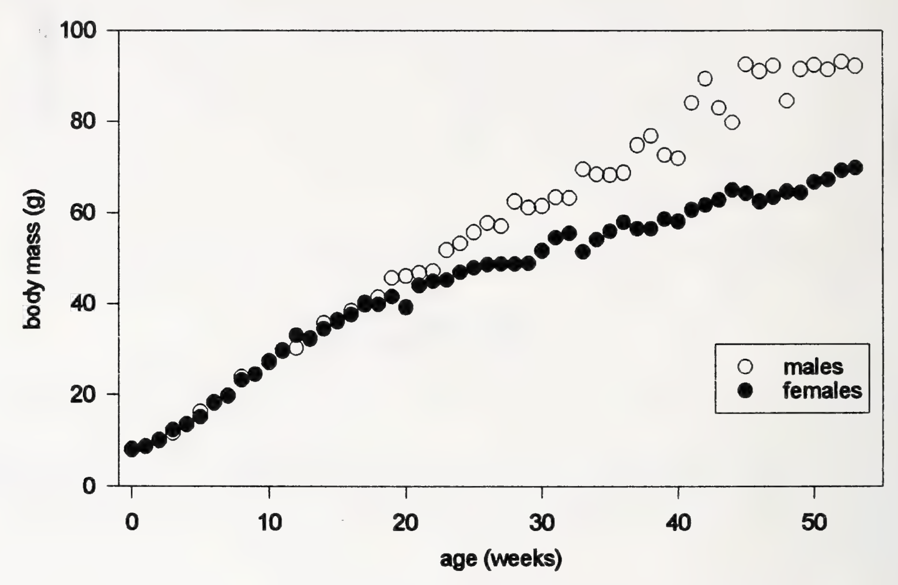


Fig. 3. Growth trajectories for males and females of Zambian common mole-rats within the first year of life.

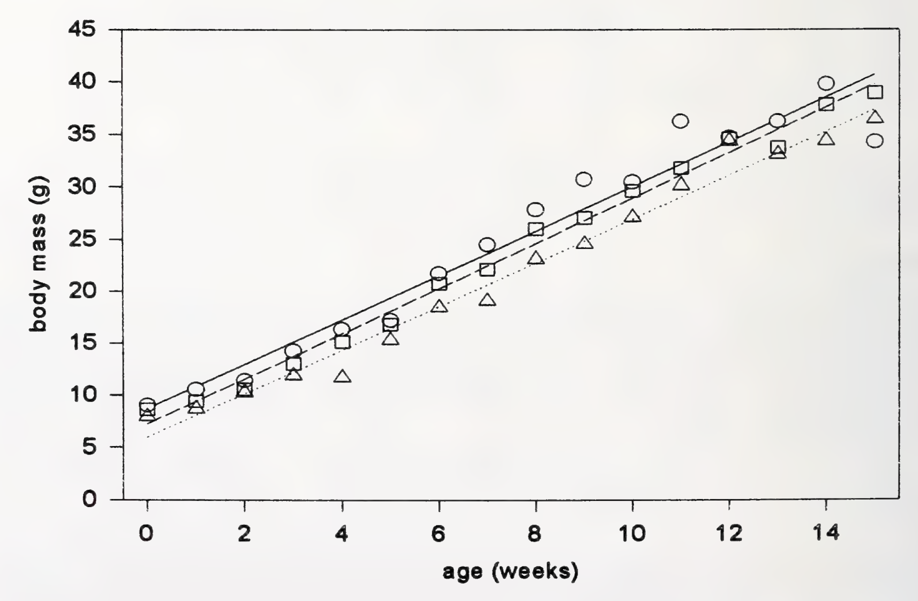


Fig. 4. Growth curves for the linear phase of growth in juvenile Zambian common mole-rats plotted for different litter sizes (circles: litter size 1; squares: litter size 2; triangles: litter size 3).

Age and size of the family

Offspring of fledgling colonies (founder pairs) required on average 53 weeks (SD = 11.4; n = 12) to reach their adult weights, while the offspring born to established families reached their adult weights in 48 weeks (SD = 12.2; n = 12). This difference was, however, not significant (two-tailed t-test; P = 0.302). The analysis of weight data for the linear (juvenile) phase of growth showed no significant differences in growth rates of pups born to pairs and offspring born to families (parents plus elder siblings). In the same way, there were no correlations between the growth rate in the juvenile phase, on the one hand, and order of litter (r = 0.0176; P = 0.868; n = 92) or age of mother (r = 0.298; P = 0.784; n = 43) on the other hand.

Sucklings whose mothers became pregnant during (early phase of) lactation grew at the same rate as those whose mothers were non-pregnant (two-tailed t-test, P = 0.138).

Table 5. Growth parameters of Zambian common mole-rats estimated according to the Gompertz equation.

	females (n = 10) mean (SD)	males (n = 7) mean (SD)
asymptotic value (A) (g)	80.2 (13.3)	131.7 (18.2)
growth constant (K) ($days^{-1}$)	0.0065 (0.0023)	0.0061 (0.0015)
age at the inflection point (I) (days)	81.0 (18.7)	148.1 (14.3)
maximum growth rate ($K\,A\,e^{-1}$) (g/day)	0.182 (0.041)	0.292 (0.079)
determination coefficient (r^2)	0.95 (0.02)	0.96 (0.03)

Discussion

The data analysed in this study have not been collected with the intention to address and assess all the possible effects upon reproduction and development. In fact, the study can be considered a by-product of other studies. Due to manipulations of the family size (removal of animals for morphological studies or in order to found new families) there was never a new litter born to a family consisting of more than 14 grown-up animals. Because of these reasons some variables (like the age of the mother, its reproductive experience, and the size of the colony) cannot be separated from each other, and their effect on growth cannot be tested.

Of course, we cannot exclude that reproductive and growth characteristics of captive *Cryptomys* differ from those of wild animals. Since, however, virtually all the published data on reproductive biology in bathyergids were obtained on captive individuals, our results can be compared with those of other authors on other species. The uniformity of growth in the linear juvenile phase (irrespective of the litter size and gender) indicates that at least this parameter is, however, very conservative, species-specific and independent of animal maintenance conditions.

Litter size

It is apparent that any analysis of a small sample may not reveal the maximum possible litter size. Similarly, if we had studied only two particular multiparous females, the mean

litter size for the Zambian mole-rat would have appeared to be higher. Our data set does not allow to distinguish whether the observed tendency for increase of the litter size in some females was an effect of their multiparity or the effect of a larger family size with more helpers. (Of course, all animals were fed ad libitum, so the effect of helpers would be only indirect).

Our experience indicates that statements like the following are not tenable if based on a small study sample. "It is of interest that the species producing the smallest litters (e. g., Zambian common *Cryptomys* or *C. mechowi*) are found in tropical central Africa where temperatures are equable and rainfall is predictable. ... These optimally favourable conditions in turn would not lead to selection for large sized colonies" (Bennett and Aguilar 1995). Additionally, it should be noted that, contrary to this statement, optimally favourable and predictable conditions lead, at least in short terms, to selection for large sized colonies both in captivity and in the field. Note, e. g., that the largest colony sizes of naked mole-rats (about 300 animals) have been found in cultivated sweet potato fields and not in semideserts with widely spaced geophytes (cf., Brett 1991).

Sex ratio

The sex ratio of neonates was skewed in favour of females (M : F = 0.85). Since the mortality of male neonates (31.6%) was higher than in females (20%), it is highly probable that the neonates which died or were killed and eaten by the mother before being sexed, were largely males. If so, the sex ratio of neonates would be more balanced, yet the postnatal mortality of males would still be larger than established here. Assuming that the sex ratio at conception and that of unidentified neonates was about equal, the findings would imply a high male prenatal mortality which continues after birth. This conclusion seems to be corroborated by our records on the sex ratio (80 M : 104 F = 0.77) of subadult and adult Zambian common *Cryptomys* of the same species captured in the field (Burda 1989 plus unpublished data of Scharff 1996).

Growth rate

Bennett et al. (1991, 1994), Bennett and Aguilar (1995) paid particular attention to the value of the growth constant (K) and related it with sociality. The authors found higher K (0.04–0.05/day) in solitary mole-rats, lower K (0.01/day) in social mole-rats. Following their argument, we conclude that very low growth constants (0.006/day) as established here for Zambian common mole-rats would give evidence of high sociality in this species. Bennett et al. (1991) also provided the mean growth rates (actually the authors should speak of maximum instead of mean growth rates) of 1.2–3.3 g/day in solitary and about 0.2 g/day in social bathyergids. Again, the values counted in the present study for Zambian common mole-rats (0.2–0.3 g/day) would rank these animals to highly social species. However, we hasten to add that employing the Gompertz equation and computing growth parameters from data that do not take the complete growth period into account leads to errors (for mathematical reasoning and experimental evidence, see Begall 1997).

The ecological aridity hypothesis predicts that the first litters born to pairs would be larger and would grow faster than subsequent litters, as there is a necessity for fast recruitment of a large work force in fledgling colonies. Indeed, Jarvis et al. (1991) found evidence for a faster growth rate in the first litters born to pairs in *H. glaber*. Bennett et al. (1991) reported the same phenomenon for *C. damarensis*. Our data, demonstrate, however, that one should be very cautious to make similar conclusions when based on small sample sizes. In any case, the data for the Zambian common mole-rat are in contrast with the prediction or, at least, they do not support it.

The independence of the developmental rate on the litter size, family size, age or reproductive history of the mother gives evidence for a conservative rather than plastic (and hence adaptive) nature of this trait. Consequently, we may assume (or at least we cannot exclude) that the slow developmental rate is one of the causes rather than a consequence of (eu)social way of life in some bathyergids.

Maternal investment

Two results obtained in this study are of special interest: Firstly, pups conceived during lactation had significantly lower birth weights than others; secondly, sucklings of pregnant mothers grew at the same rate as those of non-pregnant mothers. This indicates that pregnant mothers which were (still) suckling the pups of the previous litter invest less in their yet unborn pups. This finding is in concordance with theoretical prediction that mothers should invest more into those offspring, in which larger investments have been made already.

Zusammenfassung

Reproduktive Charakteristika und Wachstum bei eusozialen Kleingraumullen aus Sambia (Cryptomys sp., Bathyergidae)

Reproduktion, Wachstum und Mortalität wurden an in Gefangenschaft gehaltenen sambischen Kleingraumullen (*Cryptomys* sp.) statistisch untersucht. Die Tragzeit betrug 98 Tage (von 84 bis 112 Tagen). Die durchschnittliche Wurfgröße lag bei 2,4 (SD = 0,9; n = 102), wobei zwischen 1 und 5 Junge geworfen wurden. Große Würfe waren selten, kamen aber bei zwei multiparen Weibchen recht häufig vor. Das Gewicht der Neugeborenen lag zwischen 5,7 g und 10,7 g – im Durchschnitt bei 7,9 g – und war negativ mit der Wurfgröße korreliert. Die Sterblichkeitsrate der Neugeborenen betrug ca. 34% und war bei den Männchen höher als bei den Weibchen; dadurch ergab sich 8 Wochen nach der Geburt ein Geschlechterverhältnis von 0,73 : 1 (n = 159). Innerhalb der ersten 20 Wochen war das Wachstum nahezu linear (mit einer durchschnittlichen Wachstumsrate von 0,27 g/Tag) und unabhängig von Geschlecht, Wurf- und Familiengröße. Die nach der Gompertz-Gleichung berechneten Wachstumskonstanten waren sehr niedrig (K = 0,006; n = 17). Durch die vorliegende Untersuchung konnte die Vorhersage der Ariditäts-Hypothese („die ersten Würfe eines Paares wachsen schneller als Junge, die in etablierten Familien geboren werden“) zur Begründung der Eusozialität bei Graumullen nicht bestätigt werden. Trächtige und gleichzeitig laktierende Muttertiere investieren offensichtlich mehr Energie in die Säuglinge als in die Embryonen. Das Wachstum und die Entwicklungsrate der sambischen Graumulle sind eher als konservative und nicht als apomorphe Merkmale zu interpretieren. Wir können annehmen (oder zumindest nicht ausschließen), daß die langsame Entwicklungsrate eine der Ursachen und nicht eine Folge der (Eu)Sozialität ist.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Two new karyotypic forms of *Spalax leucodon* (Nordmann, 1840) (Mammalia: Rodentia) from Turkey

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Key words: *Spalax leucodon*, karyology, Turkey

The subterranean mole rats belonging to the family Spalacidae are distributed in southeastern Europe, Asia Minor, Caucasus, Transcaucasus, Ukraine, Armenia, Syria, Palestine, Iraq, Israel, Jordan, and northeastern Africa (Ognev 1947; Ondrias 1966; Lay and Nadler 1972; Corbet 1978; Giaga et al. 1982; Nevo 1991; Harrison and Bates 1991). As yet, about 40 chromosomal forms of *Spalax* have been reported in the literature from these areas.

According to the most recent morphological studies there are two species (*S. leucodon* and *S. ehrenberg* and nine subspecies (*S. l. nehringi*, *S. l. armeniacus*, *S. l. cilicicus*, *S. l. anatolicus*, *S. l. turcicus*, *S. l. tuncelicus*, *S. e. intermedius*, *S. e. kirgisorum*, and *S. e. nevoi*) of blind mole rats in Turkey (Kivanç 1988; Coşkun 1996 a, b). However, the results from karyological studies revealed seven karyological forms (2 n = 38, 40, 50, 54, 56, 60, and 62) of *S. leucodon* and four karyological forms (2 n = 52, 54, 56, and 58) of *S. ehrenbergi* in Turkey, and the number of chromosome arms (NF) for *S. leucodon* and *S. ehrenbergi* varied from 74 to 82 and from 72 to 90, respectively (Soldatovic and Savic 1978; Savic and Soldatovic 1979; Yüksel 1984; Gülkaç and Yüksel 1989; Yüksel and Gülkaç 1992, 1995; Nevo et al. 1994, 1995; Ivanitskaya et al. 1997). Nevo et al. (1994, 1995) stated that each of the chromosomal forms is a separate biological species. They also examined the populations using Nei's genetic distance between populations obtained by allozyme electrophoresis and claimed that some populations having identical diploid chromosome numbers are different biological species, presumably representing about 20 such species in Turkey.

The karyotypes of 4 specimens from Sebil and 3 specimens from Gülek belonging to *Spalax leucodon* were analysed here (Fig. 1). Chromosome preparations from bone marrow were made in accordance with Ford and Hamerton (1956), and about 30 metaphase cells of each animal were examined. The karyotype preparations and animals examined were deposited in the Department of Biology, Faculty of Science, University of Ankara.

The diploid karyotype of the Sebil population is composed of 2 n = 52, NF = 72, NFa = 68. The X chromosome is a medium sized submetacentric, and the Y chromosome is a small acrocentric. The autosomal set can be divided into three groups: 3 pairs of submetacentrics, 6 pairs of subtelocentrics and 16 pairs of acrocentrics (Fig. 2).

The Gülek population has 2 n = 56, NF = 72, and NFa = 68. The X chromosome is a medium sized metacentric, and the Y chromosome is a small acrocentric. The autosomal set has a pair of metacentrics, 2 pairs of submetacentrics, 4 pairs of subtelocentrics, and 20 pairs of acrocentrics (Fig. 2).

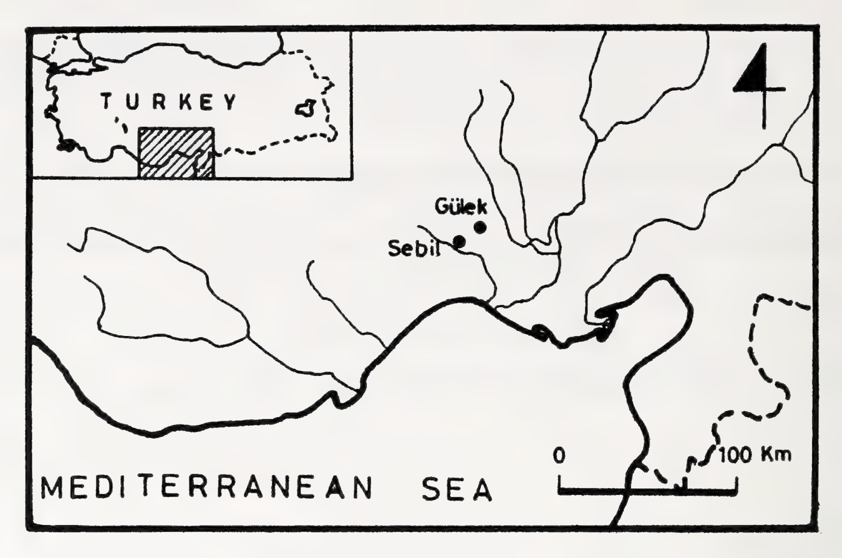
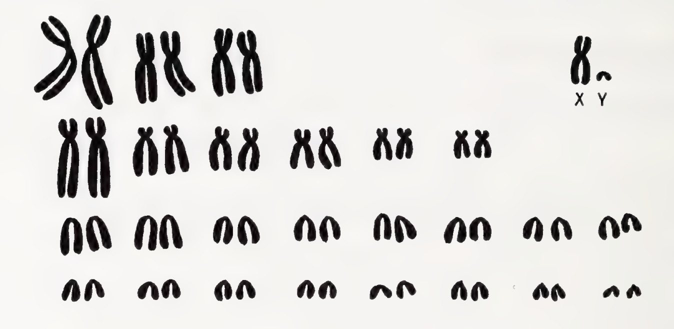


Fig. 1. The location of Gülek and Sebil in Turkey



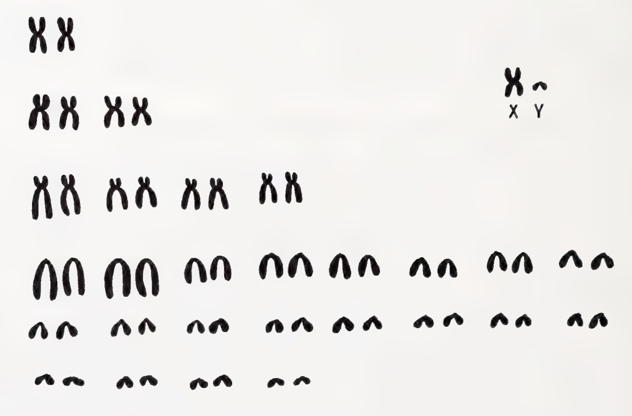


Fig. 2. The karyotype of a male *Spalax leucodon* from Sebil (a), and a male from Gülek (b)

Table 1. Chromosomal records of *Spalax leucodon* (Nordmann, 1840) and *Spalax ehrenbergi* Nehring, 1898 from Turkey.

Spalax leucodon (Nordmann, 1840)						
Locality	2n	NF	NFa	X	Y	Reference
Çorlu and Karaevli (in Thrace)	56	78	74	sm*	a*	Soldatovic and Savic (1978)
Havran and Selçuk	38	74	70	st*	a	Savic and Soldatovic (1979)
Malatya	60	78	74	sm		Ivanitskaya et al. (1997)
Malatya	60	80	76	sm	st	Yüksel (1984)
Malatya and Yazīhan	60	80	76	sm	st	Gülkaç and Yüksel (1989)
Arguvan	60	82	78	sm	–	Gülkaç and Yüksel (1989)
Kırşehir, Nevşehir and Kayseri	60	80	76	sm	st	Yüksel and Gülkaç (1995)
Yozgat	54	74	70	sm	st	Yüksel and Gülkaç (1995)
Balıkesir and İzmir	38					Nevo et al. (1994, 1995)
Beyşehir	40					Nevo et al. (1994, 1995)
Aydın, Erzurum and Sarıkamış	50					Nevo et al. (1994, 1995)
Bolu and Bingöl	54					Nevo et al. (1994, 1995)
Denizli, Pınarbaşı and Malatya	60					Nevo et al. (1994, 1995)
Kütahya, Afyon, Konya, Sivas, Ankara, Kayseri, Havza, Suşehri	62					Nevo et al. (1994, 1995)
Gülek	56	72	68	sm	a	this study
Sebil	52	72	68	sm	a	this study
Spalax ehrenbergi Nehring, 1898						
Locality	2n	NF	NFa	X	Y	Reference
Elazığ	52	76	72	sm	st	Yüksel (1984)
Adıyaman and Hilvan	52	76	72	m*	st	Yüksel and Gülkaç (1992)
Suruç	54	76	72	m	st	Yüksel and Gülkaç (1992)
Gaziantep	56	90	86	m	st	Yüksel and Gülkaç (1992)
Diyarbakır and Urfa	52	76	72			Nevo et al. (1994, 1995)
Gaziantep	58	82	78			Nevo et al. (1994, 1995)
Tarsus	56	72	68			Nevo et al. (1994, 1995)
Tarsus	56	72	68	m	–	Ivanitskaya et al. (1997)
Gaziantep	56	82	78	sm	–	Ivanitskaya et al. (1997)
Birecik, Siverek, Diyarbakır, Elazığ	52	76	72	sm	–	Ivanitskaya et al. (1997)
Urfa	52	80	76	sm	–	Ivanitskaya et al. (1997)

* m: metacentric, sm: submetacentric, st: subtelocentric, a: acrocentric

The diploid karyotype of *Spalax leucodon* in Turkey varies between 2n = 38 and 62, NF = 72 and 82, and NFa = 68 and 78. *Spalax ehrenbergi's* diploid karyotype also varies between 2n = 52 and 58, NF = 72 and 90, and NFa = 68 and 86 (Tab. 1).

The sex chromosomes are variable in both *S. leucodon* and *S. ehrenbergi*. In most populations of *S. leucodon* in Turkey, the X chromosome was described as submetacentric (Soldatovic and Savic 1978; Yüksel 1984; Gülkaç and Yüksel 1989; Yüksel and Gülkaç 1992, 1995; Ivanitskaya et al. 1997), and only in two populations of western Turkey as subtelocentric (Savic and Soldatovic 1979). The Y chromosome is acrocentric (Soldatovic and Savic 1978; Savic and Soldatovic 1979), or subtelocentric (Yüksel 1984; Gülkaç and Yüksel 1989; Yüksel and Gülkaç 1992, 1995). We found the X chromosome to be submetacentric in the Sebil population, and metacentric in the Gülek population. The Y chromosome is acrocentric in both populations. In *S. ehrenbergi* populations, the X chromosome is submetacentric (Yüksel 1984; Ivanitskaya et al. 1997) or metacentric (Yüksel and Gülkaç 1992; Ivanitskaya et al. 1997), and the Y chromosome is subtelocentric (Yüksel 1984; Yüksel and Gülkaç 1992).

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Contribution to taxonomy and karyology of *Meriones meridianus* (Pallas, 1773) and *Meriones crassus* Sundevall, 1842 (Rodentia: Gerbillinae) from Turkey

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Vinogradov and Argyropulo (1941), Bobrinsky et al. (1965), Lay (1967), and Heptner (1975) included all sand deserts in central Asia, Ciscaucasia, northeastern Iran, northern Caucasian, Armenia, and Nakhichevan in the distrubution area of *Meriones meridianus.* Ellerman and Morrison-Scott (1951), Hatt (1959), Lay (1967), Atallah (1977), Corbet (1978), and Harrison and Bates (1991) suggested that the range of *M. crassus* extends from Syria to Iraq and Iran. The aim of this study is to contribute to distribution, taxonomy, and karyology of these species and also provide comparative material for further investigations.

Specimens were collected from the east and south-east of Turkey between 1991 and 1994. Karyologic studies were performed by using the colchicine hypotonic citrate technique (Patton 1967). Twenty slides were prepared for each specimen to be karyotyped, and at least 30 well-spread metaphase cells from each preparation were analysed. Skins and skulls of specimens were deposited in the University of Ankara (Faculty of Science).

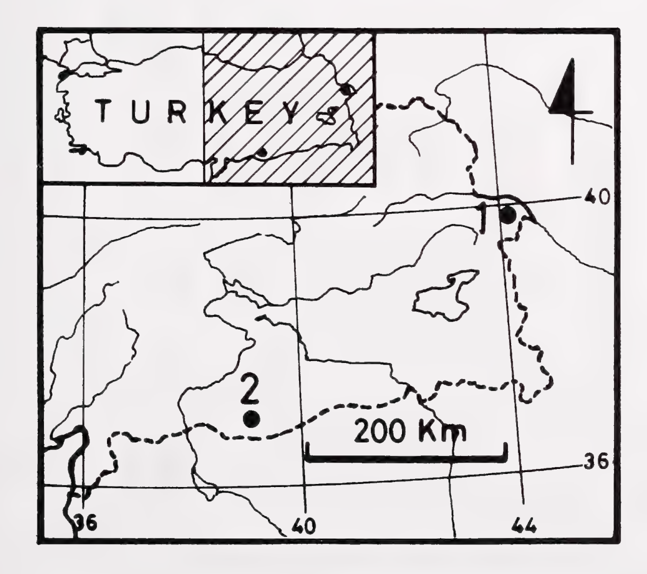


Fig. 1. Recorded localities of *M. meridianus* (1) and *M. crassus* (2) in Turkey

Meriones (Pallasiomys) meridianus (Pallas, 1773) lives in burrows with 2–3 entrances below *Equisetum ramossimum* and *Atraphaxis billardieri* bushes in sandy areas of the Aralık province in the north of Ağrı mountain (Fig. 1). Maximum total length of this species is 265 mm, and the tail is about equal to the length of head and body. External and cranial characteristics were found to be the same as described by Gamparyan and Papan-

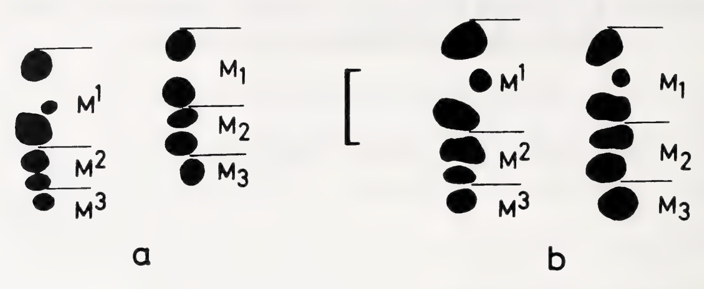


Fig. 2. Molar alveoli of *M. meridianus* (a) and *M. crassus* (b)





Fig. 3. Karyotype of a male *M. meridianus*, 2 n = 50, FN = 78 (above) and a male *M. crassus*, 2 n = 60, FN = 76 (below)

YAN (1964), and HEPTNER (1975). But, in contrast to these descriptions, the tail of a few specimens was dull yellowish to light brown with a less well-developed terminal tuft. However, there is usually a well-developed terminal black tuft on the tail. Additionally, one specimen had a black terminal tuft with a white tip. Molars are weakly hypsodont. M_1, M^2, and M_2 bear two roots, M_3 and M^3 one, and M^1 three (Fig. 2 a). The base of the proximal baculum resembles an irregular pentagon, and the length of the proximal baculum varies from 3.9 mm to 4.1 mm in adult specimens. GAMPARYAN and PAPANYAN (1964) pointed out that *M. m. dahli* was the darkest subspecies of *M. m. meridianus* in coloration, and noted that the tail was shorter than the head and body length. The characteristics given by VINOGRADOV and ARGYROPULO (1941), GAMPARYAN and PAPANYAN (1964), and CORBET (1978) are consistent with Turkish specimens. Only when characteristics given by these authors as well as geographic proximity are taken into account, it can be stated that Turkish specimens of *M. meridianus* are identical to *M. m. dahli*, even if there are variations of tail hairs, base of belly hairs, and soles of hind feet. The diploid number of chromosomes (2 n) in *M. meridianus* is 50, and the fundamental number (FN) is 78. The karyotype shows 28 meta-submetacentric and 22 acrocentric chromosomes. X and Y chromosomes are both submetacentric (Fig. 3). VORONTSOV and KOROBITSINA (1970) described a karyotype of 2 n = 50, FN = 77 for male and FN = 78 for female *M. meridianus* with 26 meta- and submetacentrics and 22 acrocentrics. According to HEPTNER (1975), there are 10 metacentrics, 16 submetacentrics and 22 acrocentrics in the karyotype of *M. meridianus* (2 n = 50; FN = 78). He also stated that there might be a resemblance in the autosomal chromosomes and variations in Y chromosomes among subspecies of *M. meridianus*. A comparison of these data with the karyotype of Turkish populations showed that our karyological findings are consistent with the karyotype given by HEPTNER (1975)

Meriones (Meriones) crassus Sundevall, 1842 is distributed on virgin pastures and steppe areas in the Şanlıurfa province near the border to Syria (Fig. 1). *M. crassus* is also a small species like *M. meridianus*; its total length approaches 246 mm. The tail is shorter than the head and body. External and cranial characteristics are consistent with the description given by HARRISON and BATES (1991). Teeth roots are the same as in *M. meridianus*, except that M_1 bears 3 roots (Fig. 2 b). The proximal baculum is also similar to *M. meridianus*, but its base is triangle-shaped with a very slight dorsal concavity. The average length of the proximal baculum is 2.6 mm, and its length varies from 2.3 mm to 2.9 mm in adult specimens. THOMAS (1919) described the subspecies *M. c. charon*, originating from Iran near the south-east border to Turkey. This was confirmed by LAY (1967). The morphological characteristics and measurements of this subspecies are consistent with Turkish specimens, except for the tail lenght. OSBORN and HELMY (1980) mentioned a bicolour-tail in 78% of Egypt specimens; this colour variation was mostly seen in Turkish specimens. Although CORBET (1978) reported that the suprameatal triangle was closed in *M. crassus*, THOMAS (1919), CHAWORTH-MUSTERS and ELLERMAN (1947), and HARRISON and BATES (1991) stated that it was open in this species (except for *M. c. longifrons*). In our Turkish specimens this triangle was similarly open. Therefore these specimens were assigned to *M. c. charon*.

The diploid number of chromosomes and the fundamental number are 60 and 76, respectively. The karyotype is composed of 44 acrocentric and 16 bi-armed chromosomes. X and Y chromosomes are submetacentric (Fig. 3). However, diploid and fundamental number were specified being 60 and 74 by MATTHEY (1957) from animals of Iran, Syria, and Algeria by BENAZZOU et al. (1982) from those of Morocco, and by QUMSIYEH et al. (1986) from Jordan. NADLER and LAY (1967) described specimens from Iran and Egypt with diploid and fundamental numbers of 60 and 72, respectively. According to this, the diploid number of chromosomes seems stable among populations and also in Turkish specimens, whereas the fundamental number shows differences in both, Turkish and the other popu-

lations mentioned. These differences originate from the number of acrocentric and biarmed chromosomes. In this respect, the fundamental number of Turkish specimens is original to *M. crassus.*

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The karyotype of *Makalata didelphoides* (Rodentia, Echimyidae)

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Makalata didelphoides is an echimyid rodent of arboricole habits, distributed east of the Rio Negro, north of the Amazon river including the Guianas and south of the Amazon from the Rio Xingu east-ward (Emmons 1993). Its karyotype, as in most species of the family, has not been previously described. Of the 55 species of Echimyidae recognized by Honacki et al. (1982), or between 60 and 100 species according to Emmons (1990), around 20 have been karyotypically analyzed. Known diploid numbers (2 n) in this family range from 14 to 118, and the fundamental numbers (FN, sex chromosomes not included) from 16 to 118; high 2 n and FN are frequent in arboricole species, against lower numbers in terrestrial species. *Echimys armatus* (I. Geoffroy, 1838) (= *M. didelphoides*) was placed in a separate genus, *Makalata*, by Husson (1978), a classification followed by Woods (1993) but not by Emmons (1990). *Makalata didelphoides* (Desmarest, 1817) is the oldest name for the red-nosed spiny rats currently known as *Makalata armata* as shown by Emmons (1993). One of us (AL), after examining the holotype at the Paris Museum, reached the same conclusion. The aim of this study was to describe the karyotype of *M. didelphoides* and to discuss the affinities of the species using karyologic information.

Studied specimens were provided by ELETRONORTE (the Amazonian electric company of Brazil). They were collected in 1987 as part of the animal rescue program "Operação Muiraquitã" at the time of the flooding of the Balbina Hydroelectric Dam on the Rio Uatumã, State of Amazonas. Four of the 20 specimens received, two males and two females, were karyotypically analyzed. Skins and skulls of these specimens were stored at the mammal collection of the Departamento de Sistemática e Ecologia of the Universidade Federal da Paraíba (Catalog numbers: UFPB 990, 958, 956, and 959).

Chromosome preparations were obtained from bone marrow by standard techniques (Baker et al. 1982). Slides were stained with conventional Giemsa staining; G and C banding were obtained following Seabrigt (1971) and Sumner (1972), respectively. A total of 20 metaphases were analyzed, approximately 5 for each specimen. Homologous chromosomes were identified by size, shape and G banding pattern.

In the four studied animals the diploid number was 66, and the fundamental number was 106 (Fig. 1). The karyotype contained 20 pairs of metacentric chromosomes varying gradually in size, one small submetacentric pair and 11 pairs of medium sized acrocentrics-subtelocentrics with a small size variation. The long arm of pair 11 showed a secondary constriction, which is a characteristic of the family Echimyidae. The X chromosome was a large subtelocentric and the Y chromosome was a small acrocentric. The pattern of G bands is shown in figure 2. C bands (Fig. 3) were restricted to pericentromeric regions. They were not evident in the large metacentric pairs 2, 3 and 4.

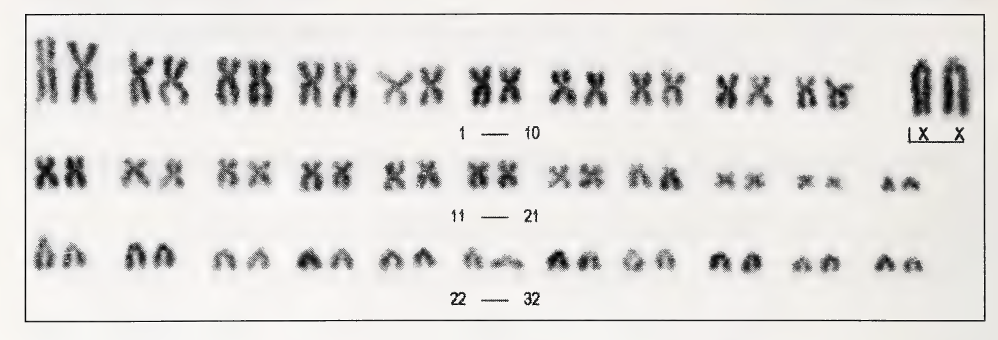


Fig. 1. Karyotype of female *Makalata didelphoides* (UFPB Nr. 956). Giemsa staining.

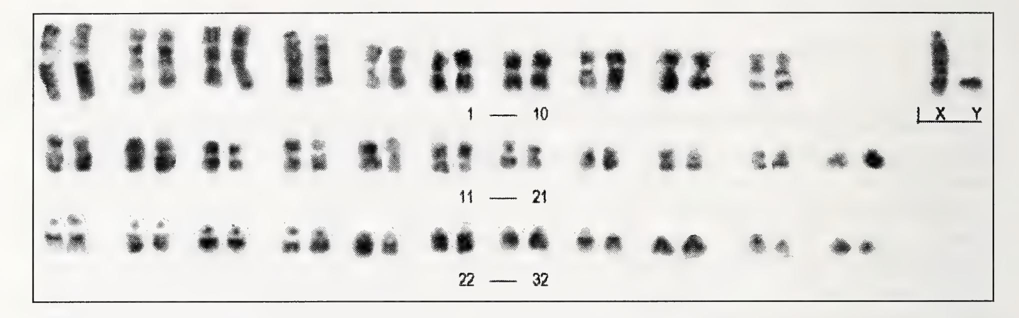


Fig. 2. G banded karyotype of male *Makalata didelphoides* (UFPB Nr. 990).

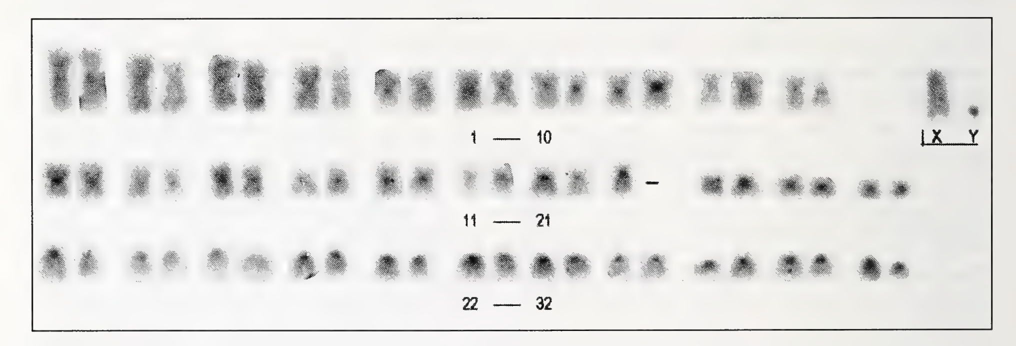


Fig. 3. C banded karyotype of male *Makalata didelphoides.* Same individual of figure 2, one chromosome of pair 18 is missing.

The karyotype of "*Makalata armata*" collected at Rio Jamari, Rondônia reported by Leal Mesquita (1991) (2 n = 70, FN = 120) differed substantially from the one here described. The specimen karyotyped by this author, deposited in the Museu de Zoologia, University of Saõ Paulo, (Nr. 27 446) is also morphologically different and belongs to a different species. Comparisons of diploid and fundamental numbers exclude simple Robertsonian mechanisms to account for these differences. More drastic karyological shuffling appears to be needed for explaining observed differences between our specimens and the one from Rio Jamari.

The karyotype of *Makalata didelphoides* shows a fundamental number within the range of most reported arboricole echimyids. *Echimys dasythrix* shows 2 n = 96, NF = 102 (I. Sbalqueiro pers. comm.); *Echimys* sp. 2 n = 90, FN = 108 (Yonenaga 1975); *Mesomys*

hispidus 2 n = 60, FN = 120 (Leal Mesquita 1991); *Isothrix bistriata* from Rio Jamari 2 n = 60, FN = 120 (Leal Mesquita 1991). However, *Isothrix pagurus* from Peru shows 2 n = 54–58, and *Isothrix* sp. from Manaus 2 n = 22, FN = 38 (Patton and Emmons 1985). J. L. Dunnum, J. Salazar-Bravo, and T. L. Yates reported in a study presented at the 76th Annual Meeting of the American Society of Mammalogists, 1996, (Abstract 111), a diploid number of 118 for *Dactylomys boliviensis*.

Variation in diploid number among arboreal echimyids appears to be higher than in fundamental number, suggesting that Robertsonian rearrangements might be significant in the karyological evolution of this group.

Despite the limited karyological data available for the genus *Echimys*, the low 2 n = 66 of *M. didelphoides* does not correspond to the high diploid numbers in known *Echimys*, and falls within the range of other genera such as *Mesomys* and *Isothrix*. This low 2 n represents another character supporting the separation of *E. armatus* (= *M. didelphoides*) from *Echimys*, as proposed by the morphological studies of Husson (1978). The shorter tail, and the frequent lingual opening of the metaflexus in not very worn upper M1 or M2, are also diverging characters proper of the genus *Makalata*.

Patton and Reig (1989), in their study of electromorphic variation in Echimyidae, did not include *Echimys* specimens. Nevertheless, they showed that *Isothrix* and *Makalata* are closer to one another than to *Mesomys*, and that these three genera form a diverging clade from terrestrial *Proechimys*. Karyological evidence supports this view and also suggests that *Makalata*, *Isothrix*, and *Mesomys* form a separate group within the subfamily Echimyinae.

More recently, Lara et al. (1996) published a valuable analysis of relationships between echimyids based on cytochrome b sequences. Their results supported the divergence of terrestrial *Proechimys* and *Trinomys* from arboreal echimyids. They also show a clade including *Echimys chrysurus*, *Nelomys* cf. *brasiliensis* and *Makalata didelphoides*. The monophyly of *Echimys chrysurus* and *Nelomys* cf. *brasiliensis* is well supported (bootstrap value 96). *Makalata*, however, is only marginally supported as sister taxon to *Echimys* + *Nelomys* (bootstrap value 57). Clades including *Makalata* and *Isothrix*, *Mesomys* or *Dactylomys* have even lower bootstrap values. The contradiction between this DNA sequence results and karyologic and electromorphic evidence requires further studies of DNA sequences based on additional samples and other species of *Echimys* and *Nelomys*.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Buchbesprechungen

Heptner, V. G.; Mead, J. G. (eds.) (1996): **Mammals of the Soviet Union**, Vol. II, Part 3. Pinnipeds and toothed whales, Pinnipedia and Odontoceti. Lebanon, New Hampshire: Science Publishers 1996. 995 pp., numerous black and white photographs and maps, some colour plates, hard cover. Price $ 225,–. ISBN 1-886106-67-3.

The anachronistic title of the English version of the book originates from the Russian edition, which was published in Moscow in 1976. The present volume has been translated for the Smithsonian Institution Libraries by P. M. Rao of the Amerind Publishing Company of New Delhi, India. Because of the diversity of participating institutions, it is difficult for the reader to cite the book correctly: The original Russian series of the three-volume "Mammals of the Soviet Union" was edited by V. G. Heptner and N. P. Naumov, the Russian version of the present volume on marine mammals was edited by the late V. G. Heptner alone; in the United States J. G. Mead was the "Scientific Editor", and V. S. Kothekar was active as "General Editor" in India.

In spite of these more technical problems, the reader and user of this book has to agree with statements in the forword to the English edition: "One of the values of this translated volume is to give English readers an insight into another philosophical system that devoted nearly a century to the studies of marine mammals. This work is important because it has an abundance of data that were taken from commercial harvest, particularly from small cetaceans, that have been generally unavailable to the English-speaking community. A monograph of this magnitude, with such an extensive bibliography, serves as an excellent entré into the Russian literature."

Generally speaking, the text is rather broad and sometimes even wordy with a slight tendency towards old-fashioned style, but the wealth of information presented from Russian sources is not easily available elsewhere to the western reader. In the text detailed information on the biology of the walrus, of one fur seal species, two species of sea lions and ten seals, as well as rich information on 30 species of toothed whales can be found.

The book covers an extremely wide geographical range, including species from the waters surrounding the northern, western and eastern shores of the Palaearctic, as well as describing two species from landlocked bodies of water, namely *Phoca caspica*, the Caspian seal, and *P. sibirica*, the Baikal seal. Both for the pinnipeds and for the cetaceans in general, a short taxonomic introduction is given, including an identification key to the Pinnipedia and a key to the cetacean suborder Odontoceti or toothed whales. Each considered family is introduced with a short diagnosis. Some general information on each considered genus is given, as well as a documentation of synonyms of species names. Thereafter a diagnosis and a detailed description of the species follows. Body measurements, external characters, and data on the skeleton are given, followed by a section on the geographic distribution of the species with an account on the geographic range in the USSR and a subsequent description of the range outside the Soviet Union. In those cases where geographical variations occur within a species, they are described in a separate section.

The main part of the chapter on each species deals with its biology. The population as a whole is characterized, data on food and daily activity, on behaviour, on migrations and their seasonality, on ontogenetic development and on growth, as well as on population dynamics are given and the field characteristics of the species are described. Information is sometimes compiled in tables. A section on the species' economic importance concludes each chapter. Maps and line drawings are generally clear and easy to read, but it has to be mentioned that the quality of half-tone illustrations is not good; very often they lack good contrast and are printed too dark.

The bibliography is 94 pages long! It is subdivided into Russian language sources and those in other languages. An index of seven pages lists the names of considered species.

P. Langer, Gießen

KINGDON, J.: **The Kingdon field guide to African mammals.** London: Academic Press 1997. Paperback 465 pp., numerous coulour and b & w figures, many tables and maps. £ 29.95. ISBN 0-12-408355-2.

At first glance this field guide is a beautiful and impressive work not only due to its colour illustrations that present the habitus of African mammals – in many cases even those inhabiting Northern Africa – but also by virtue of illustrations taken from KINGDON's series of books on East African mammals. However, as a desktop reference or as a field guide there are also considerable drawbacks that will make it difficult to use this book for these purposes: In those cases where the name of a species is known and further information is sought, an alphabetic index of scientific species or of English names is missing. The reader has to refer to the "Checklist of Species", which gives the two versions of the names in taxonomic, but not in alphabetical order. When the reader chooses to look up the description of a species, another problem may arise: The pagination is missing in many cases! For example, on the pages dealing with baboons (*Papio* spec.), the numbers of pages 34, 35 and 36 are not printed. Two other randomly chosen examples where pagination cannot be found are: Page 345 and pages 374 through 377 (four pages in sequence!). This is most surprising for a book produced by one of the world's most eminent publishing houses of scientific material!

Magnifying glasses are necessary to identify legends on maps and on some illustrations. For example, the explanatory text on the illustration depicting ,"Tooth succession in the African elephant" (page 303) is practically illegible because of considerable size reduction of the printed figure.

The reviewer feels deeply sorry for the author, who was let down by the publisher! JONATHAN KINGDON wrote a brilliant text, he presents many details on 1 150 African mammal species, especially on their ecology and their evolutionary relationships and makes information available that can generally not be found in a book of this size. May a new edition be produced by a more conscientious editorial team!

P. LANGER, Giessen

DEGEN, A. A.: **Ecophysiology of small desert mammals.** Berlin: Springer-Verlag 1997. Hardcover 296 pp., 102 figs., 56 tabs. DM 198,–, US$ 149,50. ISBN 3-540 59259-8.

In the series "Adaptations of Desert Organisms" this volume deals with the physiological diversity in relation to desert environments inhabited by small mammals weighing up to 5 kg. The author, working in the Negev in Israel, starts his book with clear and precise definitions, referring to all nouns and adjectives making up the title of his book. This introductory chapter is followed by a section, in which the author defines deserts, describes their formation and distribution on the globe and in addition deals with the types of soils that can be found. With great pleasure the reader appreciates this helpful introduction and can only express the hope that more authors of scientific publications might follow this approach!

The subsequent sections address physiological problems and emphasize their ecological implications: Body size and allometry, body temperature and heat transfer, behavioural adaptations, aspects of water balance as well as of energy requirements and, finally, reproduction. Respiratory or sensory physiology are not considered in this book, nor are endocrinological aspects. However, this does not at all diminish the value of this book. A publication such as the present one has to rely heavily on data published in the literature and small mistakes can thus be overlooked. For example, it is highly doubtful that energy loss via combustible gases – mainly methane – "could be considered to be zero in monogastric animals" (page 163). On page 170 the author mentions herbivores that use segments of the large intestine as fermentation chambers, which in many cases also means methane production.

The book is illustrated by a diversity of line drawings – mostly diagrams – and many tables. According to the most impressive amount of data referred to in this book, the list of references encompasses 29 pages! A subject index of five pages concludes this very informative book, which not only presents a remarkable review of ecophysiological aspects of small mammals inhabiting deserts, but which can also be used as a very thorough introductive textbook!

P. LANGER, Giessen

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Individual migration between colonies of Greater mouse-eared bats (*Myotis myotis*) in Upper Bavaria

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Abstract

Dispersal between 22 nursery colonies of *Myotis myotis* was studied in Bavaria (Germany) from 1991 to 1993. Each year 6–7% of the observed banded females settled in colonies other than the one where they had been banded and short visits of females to other colonies were also observed. Movements occurred over a distance up to 34 km. Emigration rates in reobserved bats varied between colonies from 0 to 25%. In some cases, emigration did not seem to be spontaneous but may be caused by environmental factors such as unfavourable climatic conditions at the roost.

Key words: *Myotis myotis*, dispersal, emigration, cave bats

Introduction

Central European females of *Myotis myotis* form nursery colonies in attics between April and August while adult males live separately at individual roosts. Observations of banded individuals showed that movements between colonies occurred up to a distance of about 30 km and that 3 to 26% of all recaptured females migrated to other colonies (Eisentraut 1960; Felten and Klemmer 1960; Haensel 1974; Hanák 1989; Horácek 1985; Hurka 1988; Oldenburg and Hackethal 1989; Roer 1968, 1988). However, these observations do not indicate whether the controlled sample was representative of the studied population, and roost sites were not observed systematically. As a result it is not known how many migrants were only brief visitors to the alien colonies and how many were permanent settlers. Also it is unknown whether bats moved spontaneously or whether movements were triggered by external events. Casual observations suggest that bats may move to an alternative roost, if they are disturbed by predators, e. g. martens or owls (Henkel et al. 1982; Müller et al. 1992; Rogée and Lehmann 1994).

Furthermore, banded individuals are easily overlooked in sporadic observations because bats are frequently absent from the colony for several days (Bilo 1990; Braun 1989; Gebhard and Ott 1985; Rudolph and Liegl 1990). This may be especially true for one-year-old non-reproductive females (Horácek 1985; Zahn 1995). Also, banded bats might disappear by mortality and emigrants may not move to all neighbouring colonies to the same extent. To estimate the emigration rate (versus mortality) all colonies within an area have to be observed systematically.

Some authors report that the number of movements declines with increasing distances between colonies (Gaisler and Hanák 1969; Haensel 1974; Horácek 1985) but other

factors might additionally influence immigration rate: Females may meet bats of other colonies in the foraging areas and follow them to their roosts. If this is the case, larger colonies should be known to more members of a population than smaller colonies, since the probability of meeting a member of a given colony rises with its size. In larger colonies, therefore, more immigrants and visitors should be observed than in smaller ones. However, because the probability of movements between colonies decreases with increasing discance, both size and distance must be considered.

To determine the extent of movements (emigrations, visits) between colonies the presence of banded females in 22 nursery roosts was observed in this study. Moreover, the effects of colony size and distances on immigration rate were analysed.

Material and methods

The study was conducted from 1991 to 1993 in an area of 4 000 km^2 located in the south-eastern part of Upper Bavaria, (between Munich and lake Chiemsee) where 22 nursery colonies exist (Fig. 1). Probably all colonies of the area were known because of intensive reconnaissance of potential roosts (Zahn 1995). Bats were banded in three colonies settling in churches of the villages Au (colony size 700 adult bats), Litzldorf (45 adult bats) and Beyharting (200 adult bats). Banding began between 1987 and 1990 (Audet 1992; Vogel pers. comm.) when 214 nursing or juvenile females were marked in Au and Litzldorf. 116 juvenile females of Au and 53 of Beyharting were banded shortly before weaning (end of July, beginning of August) in 1991. Additionally, 44 adult and 8 juvenile females were banded during the mating season in August and September (Zahn and Dippel 1997). Altogether, 435 females were banded in the area. The total number of females in the area was about 3 000–4 000 (Zahn 1995). While females had been banded with two or three coloured plastic rings (Audet 1992) in the previous studies, one aluminium ring (ZOOL. MUSEUM BONN) per bat was used in 1991 to follow new banding regulations. Differently coloured spots of reflective tape were fixed to the aluminium rings to identify the bats over a distance of about 2 m. Plastic rings could be identified from a distance of 3 m. 15 of the 22 nursery colonies were visited two to four times a month between May and August in 1991, 1992, and 1993. The seven remaining colonies of the study area were visited one to three times each summer. All other colonies of Upper Bavaria were checked once a year (end of July, beginning of August).

Individuals that had left their birth colony and were observed in their new colony for several times during pregnancy and parturition were considered as “emigrants”. Bats that were observed only once in another colony were classified as “other migrants”. “Other migrants” includes bats that were never seen again after the observation and others that were found again at the banding site after their visit to another colony.

For correlation analyses Kendall’s Tau was used. To analyse whether larger colonies are known to more members of the population than smaller ones and to determine the influence of the migration distance, the following partial correlations were calculated (Zöfel 1992): correlation between the number of “immigrants plus other migrants” in a colony and its size (distance mathematically constant) and correlation between the number of “immigrants plus other migrants” in a colony and the distance of the colony where the “immigrants/other migrants” had been banded (colony size mathematically constant).

It was not possible to determine the origin of 5 migrating bats (Au or Litzldorf) that had lost plastic rings or chewed off parts of the reflective tape. Therefore data of Au and Litzldorf were combined to include these cases into the correlation analyses. A point located at half the distance between both villages (7 km) was regarded as the origin of the individuals. Therefore, the distance a bat had moved can be over- or underestimated up to 3.5 km.

Additionally data from Bohemia (Czech Republic) published by Horácek (1985) were analysed. He gives the number of emigrants from the colony at Beroun that were found in five other colonies. The colony sizes, the distances to Beroun, and the numbers of migrants were (size-km-number): 250-16-11, 150-4-9, 70-8-4, 50-11-4, and 40-25-1.

Results

Reobserved bats

170 of all 435 marked females were observed at least once during the years after banding. The majority of them (84%) was resident at the banding site. However, 27 (16%) of the 170 bats were found in colonies different from those where they had been marked. Fourteen (52%) of them were "emigrants" and thirteen "other migrants". Eleven of those "other migrants" were found in alien colonies before the period of parturition.

For 22 of all 27 bats (nine "other migrants" and 13 "emigrants"), it was possible to identify the colony where they had been banded. Eight females were marked in Beyharting, eight in Au, and six in Litzldorf (Fig. 1). The remaining five bats were observed in colonies where no bats had been banded but the banding site (Au or Litzldorf) could not be specified. Bats had moved as far as 34 km (two specimens) with the remaining bats moving between seven and 30 km. The average distance was 15 km.

During each year of the study, 6% to 7% (5–9 individuals) of all observed banded females lived permanently in another colony than the one in which they had been marked. 4% to 7% (3–9 individuals) of banded bats were observed as "other migrants" in other colonies each year.

The percentage of emigrated females among the 170 bats recovered in the years after banding was much lower in the large colony of Au than in the smaller colonies of Litzldorf and Beyharting (Tab. 1).

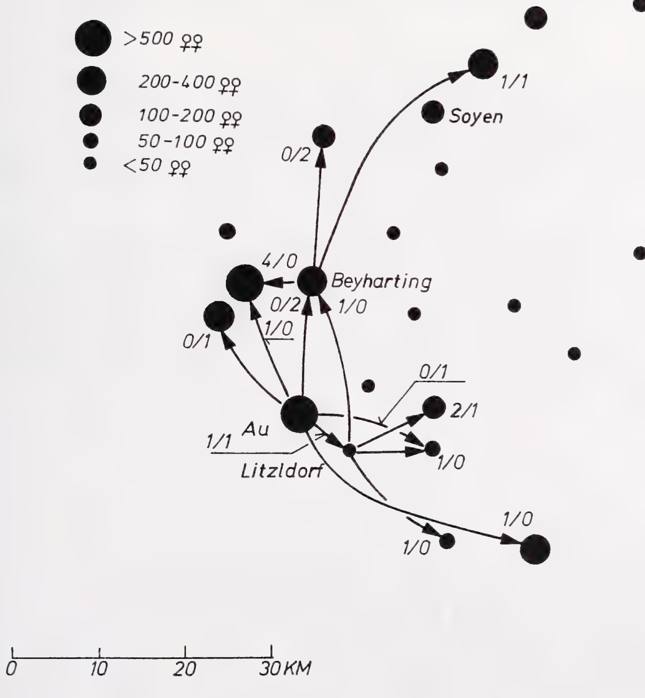


Fig. 1. Movements between colonies of *Myotis myotis* in the study area in Bavaria (1991–1993). All colonies of the area are marked by a circle. The banding sites are indicated by the names of the villages Au, Beyharting, and Litzldorf. The colony at Soyen where the emigration of many unbanded bats was observed is also named. The size of the colonies (number of adult females) is indicated by the size of the circles. The number of movements (immigrants/other migrants) is given beneath the arrows.

Table 1. Emigration rates in reobserved female *Myotis myotis* banded in the colonies Au, Beyharting, and Litzldorf. Size of the colonies: adult bats; n: number of reobserved individuals

colony (size)	emigrants in all bats recovered after banding	emigrants in the banded juveniles observed in 1992	emigrants in the banded juveniles observed in 1993
Au (700)	2% (n = 129)	0% (n = 48)	0% (n = 40)
Beyharting (200)	24% (n = 21)	24% (n = 21)	27% (n = 15)
Litzldorf (45)	25% (n = 20)	no juveniles banded	

Ten out of the 27 bats observed in other colonies (four "emigrants" and six "other migrants") were adult (>1 year) when they had moved between sites. In the case of nine bats banded before 1991, age at migration is unknown. Five "emigrants" and three "other migrants" moved within their first year of life. The five emigrants were born in the colony of Beyharting, suggesting that juvenile dispersal differed between Au and Beyharting (Tab. 1).

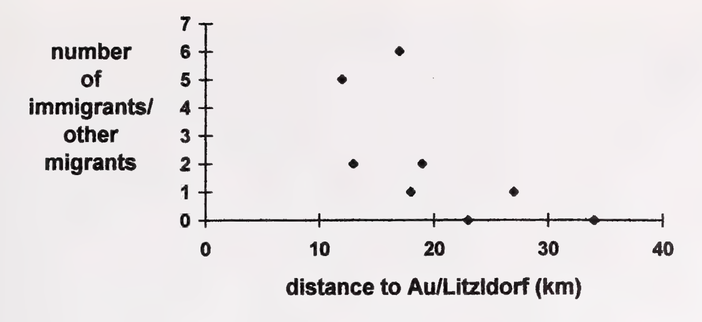
In 1993, when females born in 1991 were two years old and probably reproductive (AUDET 1992; HORÁCEK 1985), four of the five emigrated bats were still observed in their new colony. About 51 two-year-old bats settled at their banding sites (11 in Beyharting and about 40 in Au). Thus, 7% of all 55 banded two-year-old bats observed in 1993 had settled in alien colonies at the assumed beginning of their reproductive life.

Relationship between size of colony, distance of migration, and extent of immigration

The correlation analyses included all migrations from the banding sites to the neighbouring colonies within a distance of 34 km (Au/Litzldorf: 9 colonies, Beyharting: 10, Beroun: 5). All partial correlations between the number of "immigrants plus other migrants" and the size of the colony are positive (sample Au/Litzldorf: $r = 0.57$; sample Beyharting: $r = 0.46$; sample Beroun: $r = 0.96$), and all correlations between the number of "immigrants plus other migrants" and the distance from the colony, where the animals had been banded, are negative (sample Au/Litzldorf: $r = -0.70$; sample Beyharting: $r = -0.05$; sample Beroun: $r = -0.25$). However, only two of these correlations are significant ($p < 0.05$): The correlation between the number of emigrants from Beroun and the size of colony and the correlation between number of emigrants from Au and Litzldorf and distance of migration (Fig. 2 a, b).

Discussion

The majority of banded bats was not observed in subsequent years. Mortality might be much more important than migration to unknown sites in explaining their disappearance. Adult females settle permanently in colonies in summer, most colonies in the area are assumed to be known and no banded bats were found in other colonies in Upper Bavaria. The observed mortality rates in the studied colonies (59% for young and 22% for adult females, ZAHN 1995) are consistent with results of HORÁCEK (1985) and studies on other species (FINDLEY 1993). However, some immigrants in the 7 colonies that were only visited one to three times each summer might not have been detected – especially one-year-old immigrants that are absent from colonies more often than older ones (HORÁCEK 1985; ZAHN 1995). Therefore, the emigration rate of banded individuals may be underestimated.



a

number of immigrants from Beroun

0 2 4 6 8 10 12

0 50 100 150 200 250

size of the colonies

b

Fig. 2. Correlation between immigration, distance and, colony size.
a, correlation between the number of "immigrants and other migrants" in colonies of *Myotis myotis* and the distance to the site (Au/Litzldorf,) where the bats had been banded; r = 0.70. b, correlation between the number of "immigrants" in colonies of *Myotis myotis* and the colony size (banding site: Beroun; data from Horácek, 1985); r = 0.96

It is also probable that more short stays of individuals in other colonies were made than observed. In the case of females banded after fledging movements may have been misinterpreted if an individual was just visiting a colony when it was caught to be marked.

Few females settled spontaneously in another colony. A reason for the high emigration rate in Litzldorf might be the cold spring in 1991. The colony disappeared in May during a spell of cold weather which might have affected this site much more than others, due to the cool temperatures of the attic (in Litzldorf the lowest average spring roost temperature of 10 colonies settling in churches was measured (Zahn 1995)). Some banded bats, which later returned, were observed in neighbouring colonies during the cold period (Audet 1992). In June, about 40% of the colony had returned. The remainder are assumed to have settled in neighbouring colonies, because banded emigrants were observed in four of them. Climate of the roost might have caused emigration also in the colony at Soyen church (160 adult bats), located in the northern part of the study area (Fig. 1), where the highest roost temperatures of all colonies were measured (Zahn 1995). Temperatures in the church tower where the bats roosted exceeded regularly the preferred temperature range of *Myotis myotis* (Heidinger et al. 1989; Zahn 1995). In May 1993, which was extremely hot, this colony disappeared. The bats had no traditionally used roost in cooler places of the building, as other colonies (which used such sites during this time). During a cooler period in June, 65% of the bats returned. However, because no bats had been banded in Soyen, it cannot be verified that the missing females had settled in neighbouring colonies.

In 1991 there was a striking difference in the dispersal rates of young bats banded in Au and Beyharting. While the colony size of Au (no emigrants) was constant during the study, the colony Beyharting declined by 25%. About the same percentage (27%) of the females banded in Beyharting and still living in the area in 1993, settled in other colonies. This indicates not spontaneous movements of individual bats, but a long term emigration of parts of the colony in Beyharting for unknown reasons (food shortage was probably not the reason for emigration: the other colonies within the potential foraging area of 15 to 25 km (Arlettaz 1995) of the Beyharting bats did not decline or increased). Spontaneous dispersal of juvenile females seems to be very low as indicated by the bats of Au.

Females visit neighbouring colonies up to a distance of about 30 km sporadically and may settle in the foreign colony if unfavourable conditions occur at their site of birth. As in studies of Roer (1968) and Audet (1992) most short visits of bats to alien colonies were observed before the period of parturition. The maximum observed migration distance of 34 km somewhat exceeds the maximum observed distance (25 km) between colonies and foraging areas (Arlettaz 1995). The results of the correlation analyses suggest that larger colonies tend to receive more immigrants and that there is a higher exchange of individuals between closer colonies.

In southern Europe *Myotis myotis* is a perennial cave-dwelling species. A low dispersal rate may be characteristic for cave-bats. Tuttle (1976) found only 1% of female *Myotis grisescens* in home ranges of other colonies. Female *Miniopterus schreibersi* visit other colonies but all of them give birth in the colony where they were born (Palmeirim and Rodrigues 1995). *Miniopterus* and *Myotis myotis* need no dispersal to avoid inbreeding: individuals from different colonies meet at the mating sites (Palmeirim and Rodrigues 1995; Zahn and Dippel 1997). Palmeirim and Rodrigues (1995) expect strong philopatry to evolve when colonies are large and when the rate of colony extinction is low, which is the case in *Miniopterus* since caves provide ever-lasting roosts.

Because of their long time existence all caves suitable for a cave-bat species should have been colonised and occupied by the maximal number of bats which the local resources may support. Therefore, Audet (1992) expects that the average fitness of individuals should be equal in different colonies (if basic conditions as e.g. climate do not change), and that no bat can improve its fitness by moving to another colony. This may also cause the low dispersal rates in cave bats.

Buildings are less durable roosts with less constant conditions than caves. This could explain the more frequent movements in the Bavarian population of *Myotis myotis* compared to *Myotis grisescens* and *Miniopterus*. However, *Myotis myotis* settles in central European attics only since the past few hundred years. This period seems too short for an evolution of higher dispersal rates and therefore this species may keep the potential to disperse also in other areas. Studies on dispersal in south European populations could show whether dispersal patterns changed when this species extended its distribution range to the north.

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Zusammenfassung

Individuenaustausch zwischen Kolonien des Großen Mausohrs (Myotis myotis) in Oberbayern

Von 1991 bis 1993 wurde die Anwesenheit beringter Mausohren (*Myotis myotis*) in 22 Kolonien eines bayerischen Untersuchungsgebiets bei regelmäßigen Quartierkontrollen überprüft. In jedem Jahr siedelten 6–7% der beobachteten Tiere in einer anderen Kolonie als in jener, in der sie beringt worden waren. Auch wurden Kurzbesuche beringter Tiere in Nachbarkolonien festgestellt. Überflüge fanden in bis zu 34 km weit entfernte Kolonien statt. Betrachtet man alle nach der Beringung wiedergefundenen Tiere, variieren die Emigrationsraten von Kolonie zu Kolonie zwischen 0 und 25%. In einigen Fällen schienen Abwanderungen nicht spontan zu geschehen, sondern durch Umweltfaktoren wie ungünstige Klimabedingungen im Quartier ausgelöst zu werden. Größere Kolonien schienen mehr Mitgliedern benachbarter Kolonien bekannt zu sein als kleinere.

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The karyotype of *Brucepattersonius griserufescens* Hershkovitz, 1998 (Rodentia, Sigmodontinae) with comments on distribution and taxonomy

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Abstract

We karyotyped three *Oxymycterus* species (*O. hispidus*, *O. roberti*, and *O. caraparoe*) and *Brucepattersonius griserufescens. B. griserufescens* (2 n = 52/FN = 52–53) differed from the other three karyologically identical species (2 n = 54/FN = 64). Furthermore, comparisons of *O. hispidus* and *O. caraparoe* G-band karyotypes with data in the literature indicated that these species were karyologically identical with *O. roberti*, *O. angularis*, *O. rutilans*, *Oxymycterus* sp., *O. rufus*, *O. paramensis*, *O. nasutus*, and *O. akodontius.* Morphological characteristics allowed the distinction of two consistent groups, one including *O. iheringi* and *B. griserufescens*, characterized by reduced claws and a small body size, and another, of typical *Oxymycterus* species, with well-developed claws and medium or large body size. Finally, our data extended the distribution on the *iheringi* species group to Rio de Janeiro and Espírito Santo states in Brazil.

Key words: *Brucepattersonius*, *Oxymycterus*, karyotype

Introduction

Extensive karyological studies have been carried out in akodontine rodents showing striking variations in diploid chromosome number and morphology (Yonenaga et al. 1976; Kasahara 1978; Furtado 1981; Maia and Langguth 1981; Yonenaga-Yassuda et al. 1983). Within this tribe, however, the genus *Oxymycterus* is characterized by a karyotypic stability (2 n = 54 / FN = 64; Kajon et al. 1984; Vitullo et al. 1986; Svartman 1989), leading to the postulation that this genus was monokaryomorphic (Vitullo et al. 1986). Contrary to other related genera (e. g. *Akodon*) which include cryptic species, like the karyotypically distinctive *Akodon cursor* (2 n = 14) and *Akodon montensis* (2 n = 24; Yonenaga-Yassuda et al. 1975), *Oxymycterus* is characterized by distinct phenotypic differences coexisting with a marked karyological invariance.

The aim of this study was to investigate the karyotype of specimens identified as *Brucepattersonius griserufescens* Hershkovitz, 1998 and *Oxymycterus caraparoe* Hershkovitz, 1998 and compare our findings with karyological data on other related species.

Material and methods

We collected specimens of one *Brucepattersonius* and three *Oxymycterus* species from 3 different Brazilian localities: (1) Parque Nacional de Caparaó (PNC), Minas Gerais and Espírito Santo states (20°19′–20°37′ S and 41°43′–42°53′ W; altitude 1,300–2,700 m), (2) Itamonte, Rio de Janeiro State (22°23′ S and 44°38′ W; altitude 2,200 m), and (3) Parque Nacional da Chapada dos Veadeiros (PNCV), Goiás State (13°51′–14°10′ S and 47°25′–47°42′ W; altitude 700–1,500 m) (Fig. 1). Species identification was based on (1) cranial morphology, (2) body size and (3) pelage coloration. Skins and skulls were deposited in the mammals collections of the Museu Nacional (MN, Rio de Janeiro, Brazil) and the Field Museum of Natural History (FMNH, Chicago, USA).

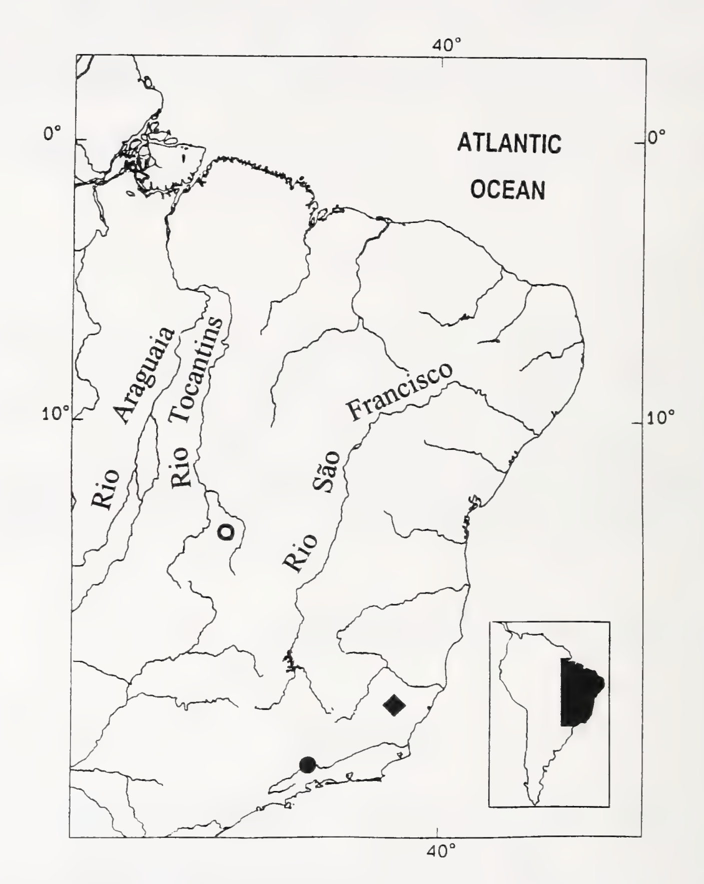


Fig. 1. Collection localities: ◆ Parque Nacional de Caparaó, ○ Parque Nacional da Chapada dos Veadeiros and ● Itamonte.

We collected 26 *B. griserufescens* from PNC (males MN 32213, 32236-37, females MN 32009-14, 32016, 32211-12, FMNH-PH 10174, 10184, 10218) and Itamonte (males LG 104, 108, 111, VPF 49, CRB 1337, 1338, females VPF 82, 86, CRB 1299, 1330, 1331). Nine *Oxymycterus hispidus* were collected from PNC (males MN 32002-06, FMNH-PH 10128, females MN 32007-08, FMNH-PH 10353). Thirty two *Oxymycterus caraparoe* were collected from PNC (males MN 31983-87, 31991, 31996, 31998, 32000, 32204, 32235, FMNH-PH 10060, 10094, 10154, 10211, females MN 31989-90, 31993-95, 31997, 31999, 32203, FMNH-PH 10069, 10168, 10421, MN 31992) and Itamonte (females, field number VPF 48, 51, LF 2178, 2170, 2172). Twenty six *Oxymycterus roberti* were collected from PNCV (males, field number CRB 1011, 1091, 1118-19, 1121, 1123, 1130, 1132-34, 1139, 1150, and females CRB 1090, 1102-03, 1105, 1116-17, 1120, 1128-29, 1131, 1135, 1137, 1147, 1151).

We karyotyped 12 *B. griserufescens* (MN 32009, VPF 49, 82, 86, LG 104, 108, 111, CRB 1299, 1330, 1331, 1337, 1338), 3 *O. hispidus* (MN 32006, 32007, FMNH-PH 10128), 5 *O. caraparoe* (MN 31987, 31993, FMNH-PH 10168, LF 2170, 2172) and 18 *O. roberti* (CRB 1103, 1105, 1116, 1117, 1118, 1119, 1120, 1121, 1123, 1128, 1129, 1130, 1131, 1132, 1139, 1147, 1150, 1151). Chromosome preparations were obtained from bone marrow cultures in RPMI 1640, 20% foetal calf serum, ethidium bromide (5 µg/ml) and colchicine 10^{-6} M for two hours or from primary cultures of kidney epithelium in Dulbecco MEM medium with 10% foetal calf serum following 5 hours of colchinization with ethidium bromide for the last 2 hours. C- and G-banding was carried out as described by Sumner (1972) and Seabright (1971), respectively.

Results

Species identification and habitat

Specimens were identified and classified by cranial morphology, and, additionally, by simple external characteristics. *O. hispidus* and *O. roberti* are large body-sized species (mean weight of captured specimens = 87.2 g and 88.6 g, respectively). They can be distinguished from one another by pelage coloration; the former by its grayish belly and the latter by its yellow-orange belly. *O. caraparoe* is a medium body-sized species (mean weight = 44.8 g) with a yellowish belly and *B. griserufescens* is a small body-sized species (mean weight = 25.1 g) with a gray to gray-yellowish belly. Identification of specimens captured in PNC was confirmed by Prof. Philip Hershkovitz (pers. comm.).

Specimens were captured in the following phytophysionomies: *O. roberti* in "campo úmido" and "vereda" (at altitudes of 700 and 1,200 m); *O. hispidus* in sub montane forest (at 1,000 to 1,300 m); *O. caraparoe* in mountain scrub and humid mountain forest (at 1,800 to 2,700 m); and *B. griserufescens* in mountain scrub, humid mountain forest, and sub montane forest (at 1,300 to 2,700 m). These findings extended the distribution of specimens similar to *O. iheringi* to Rio de Janeiro and Espírito Santo states (Brazil).

Karyotypic analysis

In the single *B. griserufescens* from Caparaó and in 9 Itamonte specimens, karyotypic analysis showed 2 n = 52 / FN = 52. The autosomal complement is composed of 24 pairs of acrocentric chromosomes and 1 medium-sized biarmed pair. The X chromosome is a large-sized submetacentric and the Y chromosome is a small acrocentric. C-banding showed that heterochromatin was present at the pericentromeric region of all chromosomes and that the short arm region of the biarmed chromosome pair was entirely heterochromatic. G-banding allowed unequivocal identification of homologous chromosomes (Fig. 2). Two other *B. griserufescens* from Itamonte showed 2 n = 52 / FN = 53 due to a pericentric inversion in one member of pair N° 2. In one of these two specimens, pair N° 25 was heteromorphic due to size differences, although this variation was not present in all cells. This variation was apparently due to loss of euchromatic material in the smaller member of this autosome pair.

Karyotypic analyses of G-band chromosomes of *O. hispidus* and *O. caraparoe* showed 2 n = 54 / FN = 64; these species were karyologically identical with one another and with several, previously reported, *Oxymycterus* species (see below). Similarly, the conventionally stained karyotype of *O. roberti* was identical with them. The autosomal complement of these species is composed of 6 pairs of biarmed chromosomes (1 large subtelocentric pair, 3 medium-sized metacentric pairs, 2 small metacentric pairs) and 20 pairs of acrocentric chromosomes varying gradually in size. The X chromosome is a medium-sized submetacentric and the Y chromosome is a small acrocentric.



Fig. 2. G-band karyotype of *Brucepattersonius griserufescens* (female specimen, VPF 82). Note heteromorphic pair n° 2 due a pericentric inversion and heteromorphic pair n° 25 due to size differences.

Discussion

Our findings indicated that *B. griserufescens* was karyotypically different from all *Oxymycterus* species so far studied, and these differences are consistent with the inclusion of *B. griserufescens* in a different genus. On the other hand, karyotypic comparisons of *O. hispidus* and *O. caraparoe* showed that these two species were identical despite their evident phenotypic differences; the former being a large-sized species with a gray belly, and the latter a medium-sized species with a yellow belly. Further comparisons with published data clearly indicated that morphologically different species of this genus were karyotypically identical. This was the case with the *O. hispidus* and *O. caraparoe* studied here and *O. roberti* and *Oxymycterus* sp. from Brasília (Svartman 1989), which were also karyologically identical with *O. angularis* from Pernambuco State (Souza 1981), *O. rutilans* from Santa Catarina State (Bueno pers. com.), and *Oxymycterus* sp. from São Paulo and Paraná states (Yonenaga-Yassuda 1975). They were also identical with 3 different allopatric species (*O. rufus*, *O. paramensis*, and *O. nasutus*; Vitullo et al. 1986) and with *O. akodontius* (Kajon et al. 1984). Moreover, 2 species (*O. rufus* and *O.* aff. *roberti*) were shown to be identical by comparative protein analysis (Hamel 1985).

Our findings indicate that the genus *Oxymycterus* includes a monokaryotypic (2n = 54 / FN = 64) and morphologically consistent species group consisting of *O. akodontius*, *O. angularis*, *O. hispidus*, *O. nasutus*, *O. paramensis*, *O. roberti*, *O. rufus*, and the *O. caraparoe* from Caparaó-Itamonte, karyologically different from *B. griserufescens* with a 2n = 52 / FN = 52–53 karyotype. In addition to karyotypic attributes, morphological characteristics such as reduced claws and small body size allow for the distinction of *O. iheringi* (karyotype unknown) and *B. griserufescens* from typical *Oxymycterus* species, with stronger feet, well-developed claws, and medium or large body sizes. *Oxymycterus* are akodontine rodents adapted to semi fossorial habitats whose frontal feet are very long, curved, and sturdy (Hinojosa et al. 1987); these characteristics are shared by all *Oxymycterus* species but are not valid for *O. iheringi* and *B. griserufescens.*

O. iheringi was initially included in *Oxymycterus*, although as an atypical species of this genus (Thomas 1896). Later studies (Thomas 1909), however, included *iheringi* in a new genus (*Microxus*), a taxonomic arrangement that was later maintained by Moojen (1952). Alternatively, Cabrera (1961) included *iheringi* in the subgenus *Akodon* (*Microxus*) despite differences in geographic distribution between *iheringi* and other *Microxus* species (see Gyldenscolpe 1932). Reig (1987), however, considered *iheringi* (following Massoia and Forbes 1963) a valid *Oxymycterus* species, while *Microxus* was considered a different Akodontini genus when studying type specimens of *Microxus mimus* and *Microxus bogotensis.*

On the other hand, molecular studies showed that *Microxus* (represented by *M. mimus*) did not deserve a generic status because it grouped with several *Akodon* species while *Oxymycterus* species were tightly grouped in a distinct clade (Smith and Patton 1993) although in this report *O. iheringi* was not studied. Recent taxonomic arrangements have also re-included *iheringi* in the genus *Oxymycterus* (Musser and Carleton 1993). However, morphologic data clearly indicated that this inclusion is questionable in view of the controversial taxonomic arrangements reported in the literature. Our karyotypic and morphological data indicate that *B. griserufescens* is different from *Oxymycterus* species as postulated by Hershkovitz (1998). Its morphologic similarities with *O. iheringi* indicate that these two species must be congeneric.

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mens collected in Itamonte. We are grateful to Dr. A. Langguth for translating the summary. This work was supported by Field Museum of Natural History, Barbara Brown Research Found, IBAMA, Museu Nacional, CNPq, INCa-FAF (Brazil).

Zusammenfassung

Der Karyotyp von Brucepattersonius griserufescens Hershkovitz, 1998 (Rodentia, Sigmodontinae) mit Bemerkungen zur Verbreitung und Taxonomie

Der Karytotyp von vier Arten der Gattungen *Oxymycterus* und *Brucepattersonius* wurde untersucht: *O. hispidus*, *O. roberti*, *O. caraparoe* und *B. griserufescens*. Der Karyotyp von *B. griserufescens* (2n = 52/FN = 52–53) unterschied sich von dem der drei anderen Arten, die alle einen 2n = 54/ FN = 64 Karyotyp aufwiesen. Ein Vergleich der G-Bandkaryotypen von *O. hispidus* und *O. caraparoe*, mit Daten aus der Literatur zeigte, daß diese Arten den gleichen Karyotyp haben wie *O. roberti*, *O. angularis*, *O. rutilans*, *Oxymycterus* sp., *O. rufus*, *O. paramensis*, *O. nasutus* und *O. akodontius*. Nach morphologischen Merkmalen lassen sich zwei Gruppen unterscheiden. Eine davon umfaßt *O. iheringi* und *B. griserufescens* mit reduzierten Krallen und kleinem Körper, die andere die typischen *Oxymycterus*-Arten mit gut entwickelten Krallen und mittelgroßem bis großem Körper. Nach unseren Daten läßt sich das bekannte Verbreitungsgebiet der *O. iheringi*-Artengruppe bis nach Rio de Janeiro und den Espirito Santo Staaten (Brasilien) erweitern.

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Cytogenetics of mole rats of the *Spalax ehrenbergi* superspecies from Jordan (Spalacidae, Rodentia)

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Abstract

Karyotypes (chromosome sets and the banding patterns (G-, C- and Ag-NOR) of the *Spalax ehrenbergi* superspecies across 12 localities from Jordan are described for the first time. All mole rats from this region (excluding two individuals from Madaba with 2n = 62) have a diploid chromosome number of 2n = 60 but they display geographical variability in the number of autosomal arms (NFa = 68, 70, 72 and 74). The most widely distributed cytotype (from Madaba in the north to Wadi Musa, near Petra, in the south) has four pairs of small biarmed chromosomes. Karyotypes of two northern populations (Irbid and Zarqa) contain six pairs of small biarmed chromosomes. The intermediate karyotype with five small biarmed chromosomes is found 25 km north of Madaba, and a polymorphic population (Mt. Nebo) with five (2 animals) and four (4 animals) pairs of small biarmed chromosomes occurs between the northern and southern cytotypes. Geographical variability is also displayed by the short arm length in the first subtelocentric autosomes. All karyotypes have a similar C-banding pattern, with the exception of heterochromatin distribution in the variable first pair. Comparative analysis of G-banded chromosomes indicated that NF differentiation is due to pericentric inversions or centromere shift. Relationships between Jordanian, Israeli, and Turkish species of the *Spalax ehrenbergi* superspecies are discussed.

Key words: *Spalax ehrenbergi*, Jordan, chromosomal, differentiation

Introduction

The *Spalax ehrenbergi* superspecies occurs in the Near East from southern Turkey to Syria, Lebanon, Iraq, Israel, and Egypt with disjunction of the range in Sinai and the Nile delta. Comparative cytogenetical studies have shown that *S. ehrenbergi* consists of different allopatric chromosome forms with narrow hybrid zones in the territory of Israel (Wahrman et al. 1969 a, b; Wahrman et al. 1985). Interdisciplinary studies including cytogenetical, genetical, morphological, physiological, and behavioral peculiarities suggest that chromosome forms in this group represent good biological species, each adapted genotypically and phenotypically to a different climatic regime (Nevo 1991; Nevo et al. 1994 a, b; 1995). Seven chromosomal species of the *S. ehrenbergi* superspecies (3 from Turkey and 4 from Israel) with a different level of chromosomal differentiation are currently described (Wahrman et al. 1969 a, b; 1985; Yüksel 1984; Yüksel and Gülkaç 1992; Nevo et al. 1995). Comparative analysis of differentially stained chromosomes has made it possible to reveal the types of chromosomal rearrangements and has shown a more complicated composition of Turkish cytotypes and a relatively large cytogenetical distance between the Turkish and Israeli populations (Ivanitskaya et al. 1997). To inter-

pret the entire route of chromosomal evolution in this group, information on karyotypes from additional localities of the range (Syria, Iraq, Lebanon, and Jordan) is needed. Mole rats from Jordan are the most interesting because these populations are geographically the nearest neighbors to the Israeli populations. However, Israeli and Jordanian mole rats are separated by the Jordan and Arava rift valleys, and we might expect new chromosome forms in Jordan.

The purpose of this study was to describe mole rat karyotypes from Jordan to fill at least partially the gap in our knowledge about relationships between Turkish and Israeli *Spalax* species.

Material and methods

Mole rats (n = 69) were collected from 12 populations across their entire range in the Jordanian Mountain ridge in January and March 1996. The sampled localities and the number of individuals analysed are presented in table 1 and figure 1.

Chromosome preparations were obtained from bone marrow by a standard in-vitro method, following the yeast-stressing technique (Lee and Elder 1980). Differentially stained chromosomes were prepared by the trypsin method for G-bands (Seabright 1971) and by the BSG method for C-bands (Sumner 1972). Nucleolar organizer regions (NORs) were identified by the $AgNO_3$ colloidal-developer method of Howell and Black (1980).

Results and discussion

Karyotypes of all mole rats examined from Jordan (except two individuals from Madaba with 2n = 62) consisted of 60 chromosomes but differed in the number of autosomal arms (Tab. 1). The morphology of the sex chromosomes was stable: the X-chromosome was submetacentric and the Y-chromosome was acrocentric.

Chromosome sets of mole rats from the northern populations of Irbid and Zarqa (populations 1 and 2, Fig. 1) consisted of 8 pairs of biarmed and 21 pairs of acrocentric autosomes (NFa = 74). The short arms of the first subtelocentric pair were relatively long, usually longer than the short arms of the X-chromosome, but were variable in length (Fig. 2 a).

Table 1. Localities, sample size, diploid (2n) and fundamental (NFa) numbers for *Spalax* populations from Jordan

No. pop. in Fig. 1	Locality	N males	N females	2n	NFa
1	Irbid	5	3	60	74
2	Zarqa	3	7	60	74
3	25 km north of Madaba	3	2	60	72
4	Mt. Nebo	2	4	60	72, 70
5	Madaba	4	5	60, 62	68, 70
6	10 km east of Madaba	2	2	60	68
7	Dhiban	2	4	60	68
8	South of Wadi Mawjib	–	5	60	(70)
9	Karak	1	3	60	(70)
10	South of Mazar	1	2	60	(70)
11	8 km north of Tafila	1	2	60	70
12	Upper Wadi Musa	4	1	60	70

NFa in some populations are in parentheses because of variable morphology of the first pair of chromosomes

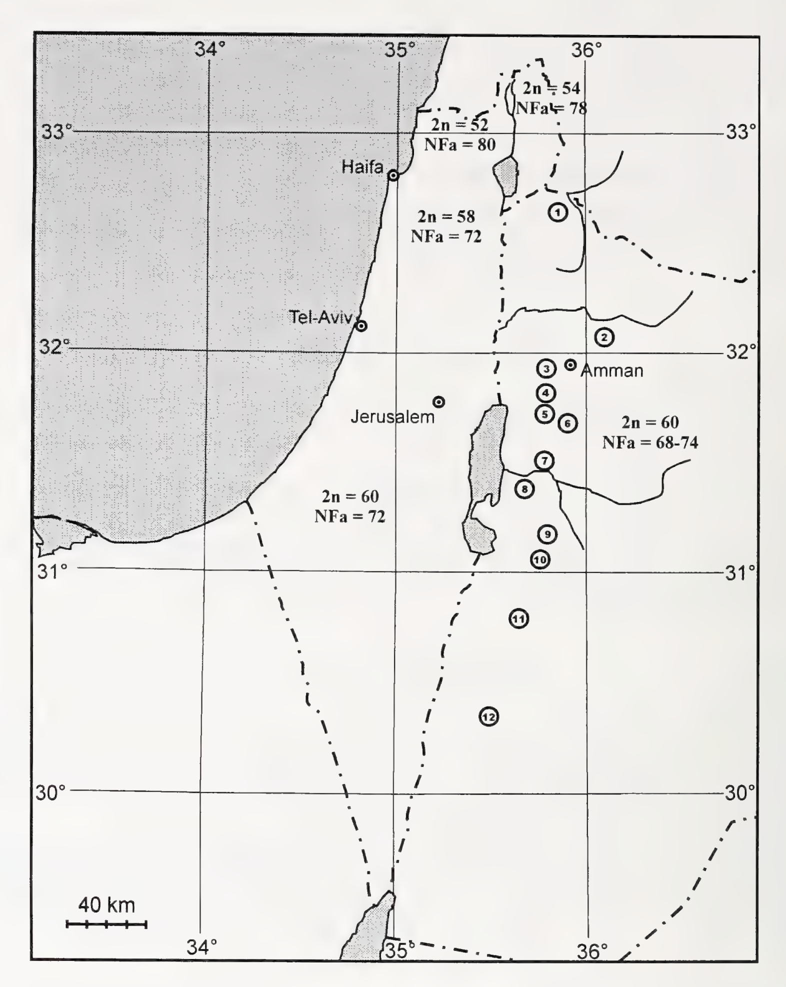


Fig. 1. Collecting localities of mole rats in Jordan and distribution of chromosome species in Israel. 1. Irbid, 2. Zarqa, 3. 25 km north of Madaba, 4. Mt. Nebo, 5. Madaba, 6. 10 km east of Madaba, 7. Dhiban, 8. south of Wadi Mawjib, 9. Karak, 10. south of Mazar, 11. 8 km north of Tafila, 12. upper Wadi Musa.

All individuals examined from population 3 (25 km north of Madaba) had 7 pairs of biarmed chromosomes and 22 pairs of acrocentrics in the autosomal complements (NFa = 72). The short arms in the first pair of autosomes were smaller than the short arms of the X-chromosome, displaying slight length variability (Fig. 2 b).

The population from Mt. Nebo was polymorphic on the number of autosomal arms caused by a different number of small biarmed chromosomes: two individuals had five pairs chromosomes in this group, and four individuals had four pairs of small biarmed autosomes (NFa = 74, 70). The first pair of chromosomes was subtelocentric but with very small short arms that were smaller than in the north of Madaba population (Fig. 2 d, e).

Almost all mole rats from populations 5, 6, and 7 (Madaba regions and Dhiban) had identical karyotypes. The variable group of small biarmed autosomes consisted of four pairs and the first pair was always acrocentrics (NFa = 68). One male and one female from Madaba had an unusual karyotype for *S. ehrenbergi*, consisting of 2n = 62, i. e. with one pair of small extra-number acrocentric chromosomes (Fig. 2 d).

All mole rats from populations 8–12 had four pairs of small biarmed autosomes but displayed geographical variability in the morphology of the first autosomal pair (Fig. 2 f, g, h). These chromosomes were subtelocentrics with short arms that were similar in length to short arms in the X-chromosome in southern populations (Tafila and Wadi Musa). The first subtelocentrics had very small short arms, sometimes invisible in conventional stained spreads, in the Mawjib, Karak, and Mazar populations. Intrapopulation and also intraindividual variability of these arm lengths were more remarkable in populations 8, 9, 10.

a

b

c

Fig. 2 a–c

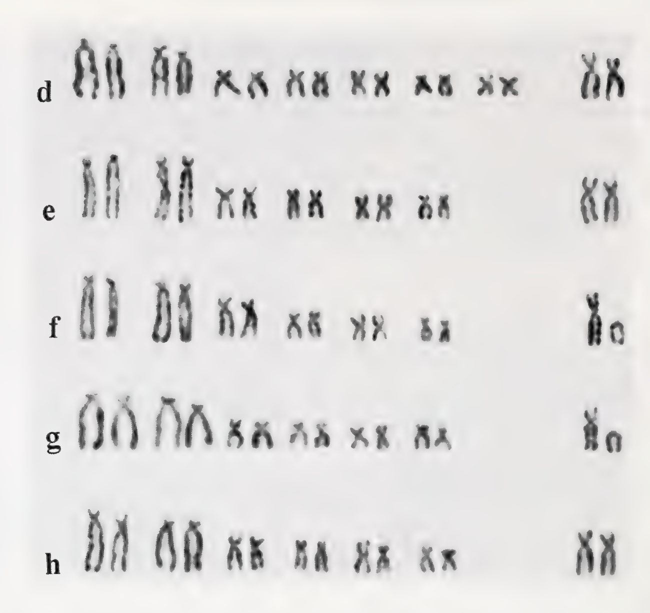


Fig. 2. Conventional stained karyotypes of some *S. ehrenbergi* cytotypes from Jordan: a female from Irbid (2n = 60, NFa = 74); b male from locality N 3 (25 km north of Madaba) (2n = 60, NFa = 72); c female from Madaba (2n = 60, NFa = 68), the small acrocentric pair in the frame is the extra-numeral chromosomes from a male karyotype with 2n = 62; d, e, f, g, h fragments of karyotypes containing biarmed autosomes and sex chromosomes of cytotypes: d female from Mt. Nebo with NFa = 72; e female from Mt. Nebo with NFa = 70; f male from Mazar; g male from Tafila; h female from Wadi Musa (2n = 60, NFa = 70).

C-banding patterns

All Jordanian mole rat cytotypes had a similar distribution and amount of heterochromatin material (Fig. 3). Acrocentric chromosomes bore more or less large blocks of pericentromeric heterochromatin; biarmed autosomes, excluding the first pair, were usually C-negative, and dot-like pericentromeric or telomeric blocks that were revealed in some of these chromosomes were unstable within population. The very small C-blocks in centromeric regions of the X-chromosomes were not as dark as in the autosomes; the Y-chromosomes were C-negative (Fig. 3 b, e). „Additional“ chromosomes in karyotypes of two individuals from Madaba did not differ in their C-banding from the other acrocentric autosomes and seem to be the smallest ones (Fig. 3 c).

The greatest interpopulation differentiation in C-banding patterns was revealed in the first pairs of autosomes. These chromosomes in cytotypes from Irbid and Zarqa bore C-blocks localized in pericentromeric and undercentromeric regions of the long arms; the short arms were C-negative (Fig. 3 a). Cytotypes from populations 3 and 4 with a variable first pair possessed pericentromeric heterochromatin and more or less intensively C-stained short arms (Fig. 3 b). The first pair in cytotype from Dhiban and Madaba was acrocentric with pericentromeric C-block and was distinguishable from the other acrocentric autosomes only by its size and the presence of two bands in the middle of the arms (Fig. 3 c). Populations from Mawjib, Karak, and Mazar were highly variable for short arm length variability in the first pair displaying both intra- and interpopulation variability in C-banding patterns of this pair. Pericentromeric heterochromatin blocks may have been absent (Fig. 3 d) or similar to C-blocks of acrocentric pairs (Fig. 3 e). The short arms and the regions close to the centromeres of the long arms were stained more

intensively than euchromatin material, differing in size and intensity (Fig. 3 d, e). The first pairs in karyotypes from the southern populations (Tafila and Wadi Musa) which were more or less stable in the morphology displayed C-banding patterns very similar to the Mawjib cytotype (Fig. 3 d).



Abb. 3 a–c



Fig. 3. Distribution of heterochromatin in different cytotypes of *S. ehrenbergi* from Jordan: a C-banding pattern in a female from Irbid (NFa = 74); b male from 25 km north of Madaba (NFa = 72), c female from Madaba (NFa = 68), the acrocentric pair in the frame is the extra-numeral chromosomes from the male karyotype with 2n = 62; d female from Wadi Mawjib (NFa = 70); e male from Karak with very small short arms in the first chromosome (NFa = 70).

G-banding patterns

G-stained chromosomes of four populations of *S. ehrenbergi* from Irbid (I) (NFa = 74), 25 km north of Madaba (N) (NFa = 72), Madaba (M) (NFa = 68), and Tafila (T) (NFa = 70) are presented in figure 4. Obviously, almost all of the chromosomes of these karyotypes displayed similar patterns of G-band sequences. The essential difference between populations concerned the group of small biarmed chromosomes. Four pairs from this group (3, 4, 5, 6) had identical morphology with the same G-banding patterns in all populations. The smallest pair (29) in karyotypes with NFa = 74 was metacentric instead of acrocentric in other karyotypes; the acrocentric condition of pair 26 in karyotypes with NFa = 74, 70, and 68 was replaced by metacentric in karyotype with NFa = 72 (group C in Fig. 4). Because of the small size of these chromosomes and the limited number of G-bands it cannot be stated with certainty what type of rearrangement (pericentric inver-

sion or centromere shift) is responsible for the change in centromeric position. Mole rats from Irbid and Zarqa (NFa = 74) differed from other populations by the biarmed condition of pair 7, which according to WAHRMAN et al. (1985) belongs to the unchangeable group A of Israeli *S. ehrenbergi*. Considering the same sequence of G-bands in acrocentric and biarmed chromosomes of pair 7, the centromere shift is a more likely type of the rearrangement.

The acrocentric condition of the first autosomal pair in the cytotype with NFa = 68 may be explained by pericentric inversion of the formerly subtelocentric chromosome with very small short arms. This is confirmed by the replacement of the dark G-band, lo-



Fig. 4. G-banding patterns of haploid sets of four cytotypes from Jordan. From left to right: Irbid (NFa = 74), 25 km north of Madaba (NFa = 72), Madaba (NFa = 68), Tafila (NFa = 70). Chromosomes are arranged according to WAHRMAN et al. (1985) classification: autosome 1–17 belong to the group A (unchangeable chromosomes in Israeli *Spalax*), autosomes 18–25 belong to the group B with Robertsonian type of rearrangement in Israeli *Spalax*, autosomes 26–29 belong to the group C with variable centromere position. Chromosome N 30 is "additional" acrocentric in a male karyotype from Madaba (2n = 62). Chromosomes 8–25 are acrocentrics; dashes indicate the centromere positions in groups A and C.

cated above centromeres in subtelocentric chromosomes, under the centromeric region in acrocentric ones. Variability of the short arm lengths in the first pair autosomes was reflected in their G-banding patterns. Relatively long arms in the cytotype from Irbid and Zarqa had numerous dark bands located close to each other, so that the short arms in these karyotypes usually resembled dark uniformly stained material. Karyotypes with small short arms of the first subtelocentric pair usually had one dark G-band adjacent to the centromeric region (Fig. 4).

Nucleolar organizing regions

Two types of N-banding patterns among Jordanian mole rats were revealed. Cytotypes with NFa = 74, 72, and 70 possessed two NORs-bearing chromosome pairs, and the cytotype from Madaba and Dhiban (NFa = 68) had one pair with NORs. These chromosomes (the first subtelocentrics and fifth metacentrics in Fig. 4) can be recognized on conventional, C-, and G-stained spreads also.

We now have more or less complete information on mole rat karyotypes from Jordan. Despite the distribution of Jordanian mole rats more than 100 km south of the Israeli *Spalax*, no variability in chromosome numbers was found in Jordan. The presence of two individuals in Madaba with 2n = 62 is unexplainable by centromeric fission, because 17 individuals with an acrocentric condition of the first pair had 2n = 60. In addition, the acrocentric morphology of the first pair in the karyotype with NFa = 68 originates from pericentric inversion (and not fission), as follows from comparative analysis of G-banded chromosomes. It is difficult to explain the reason for the appearance of the smallest "additional" acrocentric chromosomes in the *S. ehrenbergi*, karyotype. We emphasize only that this type of chromosomal polymorphism in *S. ehrenbergi* is the first on record.

The main difference among Jordanian cytotypes is caused by pericentric inversion or centeromeric shifts in four chromosomal pairs. Two of these pairs belonging to the group C. Pericentric inversions in chromosomes from this group are responsible for the NF variation among Israeli cytotypes of mole rats (WAHRMAN et al. 1985). Change of centromere position in the first and seventh pairs of chromosomes from group A in some Jordanian *Spalax* (Fig. 4) is the principal rearrangement that differentiate Israeli (2n = 60) and Jordanian mole rat cytotypes. Conventional stained karyotypes of the Israeli cytotype with 2n = 60, NFa = 72 and Jordanian cytotype from the northern Madaba population (Fig. 2 b) are seemingly identical, but G-banding method made it possible to show differentiation between them caused by an altered position of centromeres in two chromosome pairs. Furthermore, Israeli cytotypes with 2n of 52, 54, and 58 differ from Jordanian cytotypes by series of Robertsonian rearrangements.

The karyotypes of two geographically close populations form Afiq (2n = 58, NFa = 72) and Irbid (2n = 60, NFa = 74), 20 km apart, differ by one Robertsonian translocation and one pericentric inversion. The presence of biarmed condition in the 7th pair of autosomes in the Irbid and Zarqa cytotype links it with Israeli cytotypes and differentiates them from the other Jordanian cytotypes with the acrocentric morphology of this pair. The northern distribution of the Irbid cytotype is restricted by the Yurmuk river and in any case the southern Golan Afiq population with 2n = 58 is apparently a recent colonizer from the Lower Galilee mountains. The southern border of the Irbid cytotype is possibly Wadi Sir. Wadi Sir and Mt. Nebo mole rats prevail with NFa = 72. The population from Mt. Nebo is polymorphic: two of the animals had karyotypes with NFa = 72, like the northern cytotype, and four individuals had NFa = 70, karyologically identical with the southern cytotype (Mawjib, Karak, Mazar), differing from the nearby Madaba cytotype. The small sample from Mt. Nebo does not permit an explanation of the origin of chromosomal variability in this population. We cannot exclude a hybrid origin of this population, but the existence of the intergradation zone in this region is more likely.

Comparative analysis of C-banded chromosomes revealed low interpopulation variability of heterochromatin contents, except for C-banding patterns of the first subtelocentric autosome. These chromosomes in all cytotypes bear heterochromatin material, but the type of localization and its abundance yield specific patterns for different cytotypes (Fig. 3). Intrapopulation heterochromatin variability in these chromosomes is absent in the cytotype with NFa = 68, and more or less developed in cytotypes with subtelocentric morphology of these chromosomes. The higher the intrapopulation variability of the short arm length, the more changeable are the C-banding patterns. The first subtelocentric chromosomes in the Israeli *Spalax* are characterized by high variability in the length of both arms. Nevertheless, these chromosomes in all examined populations from Israel were C-negative (Wahrman et al. 1985).

In contrast to Israeli, Jordanian, and also Egyptian (Lay and Nadler 1972) species, Turkish mole rats do not possess size variability in the first pair (Ivanitskaya et al. 1997). These chromosomes in Turkish populations are either subtelocentric without remarkable variability in arm length, or acrocentric. The short arms of this chromosome in the *S. leucodon* superspecies are completely heterochromatic, and they have telomere C-bands in some 2n = 52 populations of *S. ehrenbergi*. The acrocentric condition of this pair in two Turkish cytotypes is caused by centromeric fission and not by pericentric inversion as in Jordanian cytotype from the Madaba and Dhiban region. Thus, this chromosome pair was presumably subjected to different types of rearrangements and should be excluded from the group of unchangeable chromosomes (group A in Wahrman et al. 1969, 1985). Also, chromosome pair N 7 (Fig. 4), which has an invariable biarmed morphology in the Israeli cytotypes, is replaced by acrocentric chromosomes in all Turkish species and in most Jordanian cytotypes. After combining all data on *S. ehrenbergi* karyotypes, group A will consist of 10 autosomal pairs, instead of 17 in Israeli species.

Summarizing the data on G- and C-banded chromosomes in mole rats makes it possible to conclude that the level of chromosomal divergence among Jordanian cytotypes is lower than among Turkish cytotypes, and even among Israeli mole rats. The discovery of new chromosomes involved in rearrangements in the Jordanian *Spalax* in comparison with Israeli species supports the hypothesis that more or less independent chromosomal evolution took place in these adjacent regions.

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Zusammenfassung

Zytogenetik von Blindmullen der Spalax ehrenbergi-Superspezies aus dem Jordanland (Spalacidae, Rodentia)

Karyotypen (Chromosomensätze und Muster von G-, C- und Ag-NOR-Bänderungen) der *Spalax ehrenbergi*-Superspezies aus 12 Gebieten des Jordanlandes werden neu beschrieben. Alle Blindmulle aus dieser Region (mit Ausnahme von zwei Individuen aus Madaba mit 2n = 62) hatten eine diploide Chromosomenzahl von 2n = 60, aber sie zeigten geographische Variabilität hinsichtlich der Zahl der autosomalen Arme (NFa = 68, 70, 72 und 74). Der am weitesten verbreitete Zytotyp (von Madaba im Norden bis zum Wadi Musa, nahe Petra, im Süden) hatte vier Paar kleine zweiarmige Chromosomen. Karyotypen der beiden nördlichen Populationen (Irbid und Zarqua) besaßen sechs Paar kleiner zweiarmiger

Chromosomen. Der intermediäre Karyotyp mit fünf kleinen zweiarmigen Chromosomen fand sich 25 km nördlich von Madaba; eine polymorphe Population (Mt. Nebo) mit fünf (2 Tiere) und vier (4 Tiere) Paar kleiner zweiarmiger Chromosomen kam zwischen den nördlichen und südlichen Zytotypen vor. Geographische Variabilität zeigte sich auch hinsichtlich eines sehr kurzen Armes beim ersten Paar subtelozentrischer Autosomen. Mit Ausnahme der Heterochromatinverteilung im ersten variablen Chromosomenpaar hatten alle Karyotypen ähnliche C-Bandenmuster. Eine vergleichende Analyse der Chromosomen mit G-Bänderung ergab, daß die NF-Differenzierung auf perizentrische Inversionen oder Zentromerverschiebungen zurückgeht. Die Beziehungen zwischen jordanischen, israelischen und türkischen Arten der *Spalax ehrenbergi*-Superspezies werden diskutiert.

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Reproductive biology, age structure, and diet of *Mastomys natalensis* (Muridae: Rodentia) in a Swaziland grassland

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Abstract

The time of reproduction, monthly changes in age structure and diet of *Mastomys natalensis* were investigated in a subtropical grassland in Swaziland. Mice were collected monthly over a 25 month period. The ages of *Mastomys natalensis* individuals were estimated using eye lens weight. Pregnant females and scrotal males were recorded in the wet season only, with interannual differences in the initiation of breeding being correlated with rainfall. Monthly changes in age structure of *M. natalensis* are determined by the entry of young during the wet season and the death of adults, that were previously reproductive, in the dry season. The stomach contents of *M. natalensis* consisted predominantly of vegetative plant matter in the dry season, with seeds and arthropods having contributed significantly in the wet season.

Key words: *Mastomys natalensis*, reproduction, diet, age-structure

Introduction

The multimammate mouse *Mastomys natalensis* (A. Smith, 1834) is a widespread African murid rodent of great economic importance (de Graaf 1981; Skinner and Smithers 1990). The reproductive biology and population structure of *M. natalensis* has been intensively investigated at only one study site in Tanzania (Telford 1989; Leirs and Verheyen 1995). In contrast, existing knowledge of this species in southern Africa is based on several scattered, short-term studies (Coetzee 1965; Chidumayo 1984; Bronner et al. 1988). Furthermore, the age of mice captured for these southern African studies were estimated using toothwear, a technique which is known to be inaccurate (Morris 1972).

The objectives of this study were to investigate the time of reproduction, monthly population age-structure and seasonal changes in diet of *M. natalensis* in a subtropical grassland in the Middleveld of Swaziland.

Material and methods

The study area was situated at eKundizeni Farm (26°33′ S; 31°16′ E) near Matsapha, Swaziland, approximately 1 km away from the site described in Monadjem and Perrin (1996). This region receives most of its rainfall between October and March, but the onset of rains differs between years. The mean annual rainfall recorded over 30 years by the University of Swaziland Meteorological Station, located 8 km to the east of the study site (at a similar altitude of 650–700 m a.s.l.), is 928 mm. Mean minimum temperature for July 1995 was 7.6 °C, while mean maximum temperature for February 1996 was 27.3 °C. During the study period, rainfall was recorded monthly at eKundizeni Farm.

Small mammals were trapped monthly using Sherman live-traps and commercial back-break kill-traps set in lines. The population dynamics of *Mastomys natalensis*, studied at a site approximately 2 km away, has been reported elsewhere (Monadjem and Perrin 1998). These lines were rotated on a monthly basis to avoid trapping the same line two months consecutively. Sherman traps were set on one or two nights per month from October 1995 to March 1997, whereas kill-traps were set from October 1995 to October 1997. Traps were set five metres apart and were not pre-baited. The mice captured with Sherman traps were returned to the laboratory where they were killed with chloroform, measured and their reproductive condition assessed. Reproductive condition was assessed following Leirs and Verheyen (1995). In males, the position and length of the testes, the size of the seminal vesicles and epididymal tubuli was recorded. In the females, the condition of the uterus (filiform, normal, oestrous or pregnant), the number of embryos and placental scars was recorded.

The eyes of *Mastomys natalensis* were removed immediately after death and the eye lenses were prepared for weighing following Perrin (1979). The eyes were fixed in 10% formalin. After fixation, the lenses were removed and oven dried for 7 days at 80 °C. Each lens was weighed separately on an electronic balance. The age of each mouse was estimated using the regression line of lens weight on age in days in Leirs and Verheyen (1995):

$$w = -10.46088 + 4.35076 \times \ln(a)$$

where: w = dry eye lens weight in mg; and a = age in days. Mice were assigned to one of seven age classes (< 99 days, 100–159 days, 160–219 days, 220–279 days, 280–339 days, > 340 days). *Mastomys natalensis* reaches first oestrous at a mean age of 104 days (Johnston and Oliff 1954) and, hence, the first age class includes mostly immature individuals. The remaining age classes were arbitrarily set at 60 day intervals.

Mice captured in the kill-traps were returned to the laboratory where their reproductive condition and stomach contents were assessed. Commencing in November 1996, the stomachs of the kill-trapped mice were removed for stomach content analysis following Kerley (1989) and Monadjem (1997). Four dietary categories were recognized: foliage (vegetative plant material), seeds, arthropods, and unidentified material. The importance of each food type was expressed both as a frequency of occurrence and a proportional (percentage) contribution. Frequency of occurrence was calculated as the number of stomachs in which a particular food type was observed. Percentage contribution was determined by examining the stomach contents through a dissection microscope. The relative contribution of each food type in the microscope field was estimated for five randomly placed fields.

Results

Total monthly rainfall during the study period is shown in figure 1. The total rainfall for the period October 1995 to September 1996 was 1 368 mm, and for the period October 1996 to September 1997 was 1 101 mm. Rainfall during the study period was above the long-term mean (928 mm) for the area.

The number of *Mastomys natalensis* captured in each month is shown in table 1. Other species of small mammal captured were: *Crocidura mariquensis* Roberts, *Crocidura hirta* Peters, *Rhabdomys pumilio* (Sparrman), *Mus minutoides* A. Smith, *Dendromus mystacalis* Heuglin, *Otomys angoniensis* Thomas, *Lemniscomys rosalia* (Thomas), and *Steatomys pratensis* Peters.

Reproduction

M. natalensis was not reproductively active throughout the study period (Fig. 2). Males were scrotal in 14 months of the study and females were pregnant during 8 months. Reproductive activity was correlated with rainfall in both males (r_{23} =0.802, $P < 0.001$) and females ($r_{23} = 0.569$, $P < 0.01$). Reproductive activity in females was also correlated with rainfall one and two months previously ($r_{22} = 0.622$, $P < 0.01$; $r_{21} = 0.668$, $P < 0.001$, respectively), while in males it was only correlated with rainfall one month previously ($r_{22} = 0.589$, $P < 0.01$). There was very little sign of reproductive activity, in either sex, during the dry season between April and October.

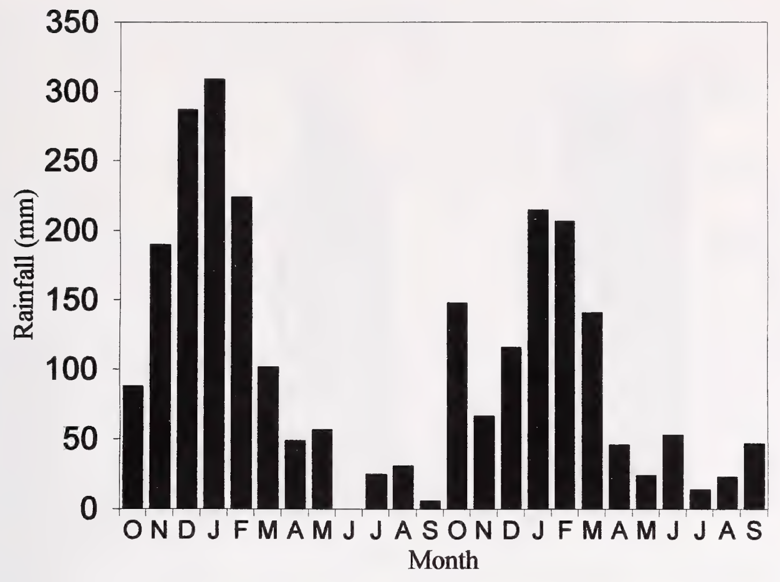


Fig. 1. Total monthly rainfall at eKundizeni Farm, Swaziland from October 1995 to October 1997.

Table 1. Number of trap-nights and number of captures of *Mastomys natalensis.*

Date	Numbers	
	Trap-nights	*M. natalensis*
1995		
October	75	6
November	45	10
December	120	5
1996		
January	80	16
February	60	5
March	120	5
April	60	11
May	60	9
June	No trapping	
July	60	10
August	60	8
September	300	14
October	150	13
November	150	15
December	150	29
1997		
January	150	5
February	150	10
March	150	8
April	40	7
May	40	8
June	40	8
July	40	5
August	40	4
September	40	4
October	40	2

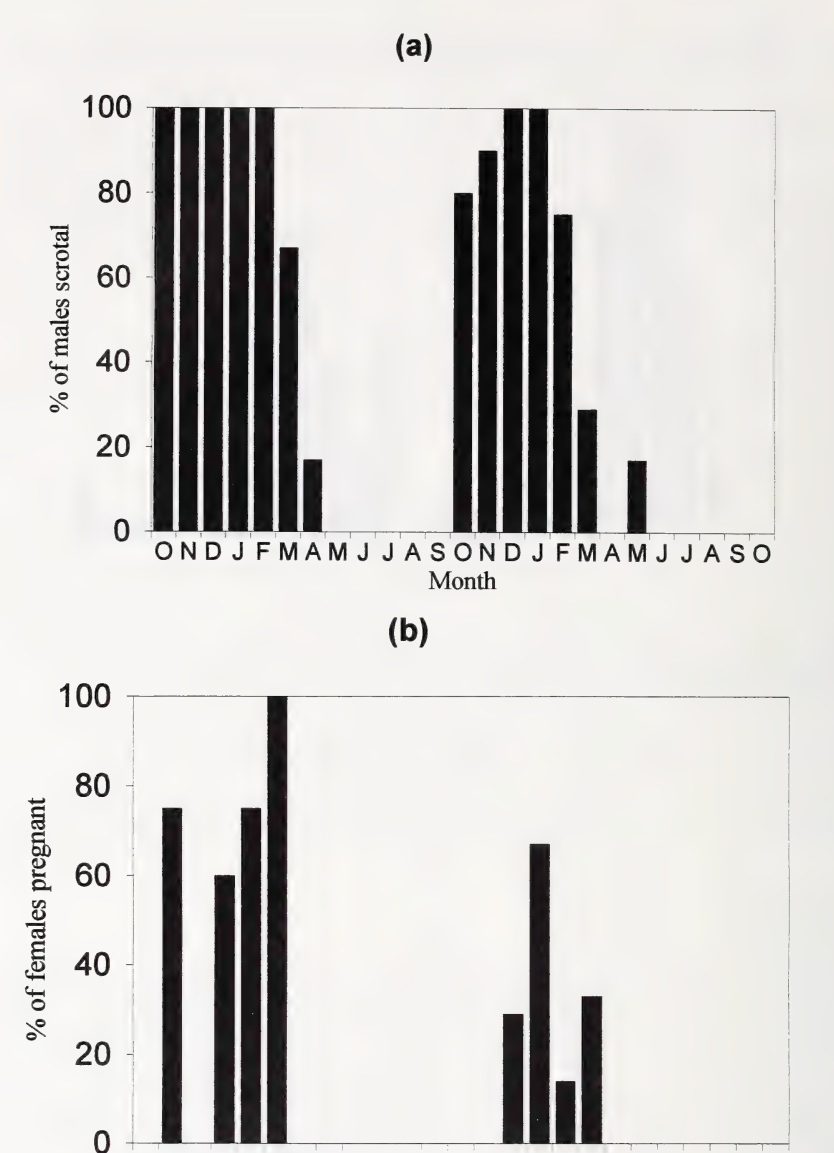


Fig. 2. The proportions (%) of *Mastomys natalensis:* (a) males with scrotal testes, and (b) pregnant females, trapped between October 1995 and October 1997.

The initiation and intensity of breeding in *M. natalensis* varied between the two years. In the 1995/6 breeding season, all males were fully scrotal at the beginning of the study in October. In the 1996/7 breeding season, however, only 80% of the males were scrotal in October. This interannual difference was even more pronounced in females, where 75% of females were pregnant in November 1995 while none were pregnant in November 1996 (and only 33% were pregnant in December 1996). Thus, *M. natalensis* initiated breeding approximately one month later in the 1996/7 breeding season than in the previous season.

Table 2. Mean mass and litter size (± SE) of female *Mastomys natalensis* of different age classes. Row values with different superscripts indicate a significant difference (ANOVA, $P < 0.05$) among age classes.

	Age class		
	<6 months	6 to 8 months	>8 months
Sample size	22	17	21
Mean mass	30.2 ± 2.6^a	30.2 ± 1.8^a	38.6 ± 1.8^b
Mean litter size	13.8 ± 2.1^a	10.7 ± 1.5^a	9.9 ± 1.6^a

The litter size of *M. natalensis* was 11.4 (n = 17; range: 3–24). There were no significant differences in the litter size of *M. natalensis* between females of ages less than six months, 6 to 8 months, and greater than 8 months (ANOVA, $P > 0.05$; Tab. 2). Females older than 8 months, however, weighed more than females in the two younger categories.

The ages of 146 *M. natalensis* (60 females and 86 males) were estimated using eye lens weight. It was thus possible to estimate the dates of birth for these individuals. Most mice were born between November and March (Fig. 3), with only a single individual being born between July and September in 1995 and none between July and November in 1996.

There was a significant, albeit weak, correlation between age and body mass in male *M. natalensis* ($r_{86} = 0.453$, $P < 0.001$).

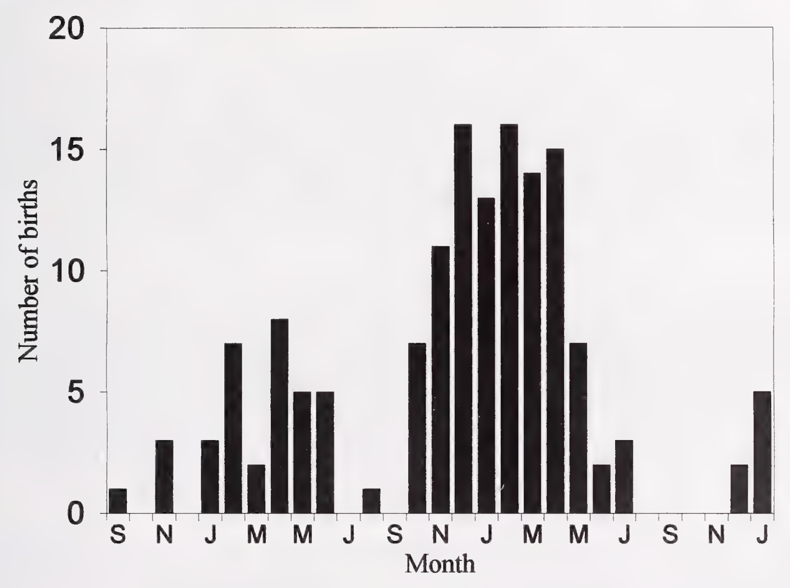


Fig. 3. Numbers of *Mastomys natalensis* born per month (based on age estimated from eye lens weight) between September 1994 and January 1997.

Age structure

The monthly age structure of *M. natalensis*, based on the mice that were aged by the eye lens weight technique, is shown in table 3. Immature mice (first age class) entered the population in December in the 1995/6 season, but only in February in the 1996/7 season. This corresponds to the delay in reproductive activity recorded in the 1996/7 season. Immature mice were recorded between December 1995 and July 1996 with a peak in April,

Table 3. Seasonal changes in age class structure of *Mastomys natalensis* between October 1995 and March 1997 at eKundizeni Farm, Swaziland. Numbers are the percentages of individuals recorded in each age class.

Month		n	Age class (in days)					
			<99	100–159	160–219	220–279	280–339	>340
1995	Oct	6	–	50	17	17	17	–
	Nov	9	–	–	33	22	44	–
	Dec	4	25	–	25	25	–	25
1996	Jan	15	20	7	7	40	13	13
	Feb	4	25	25	–	25	–	25
	Mar	4	50	25	–	–	–	25
	Apr	11	73	27	–	–	–	–
	May	9	22	78	–	–	–	–
	Jun	No data						
	Jul	10	20	40	10	20	–	10
	Aug	8	–	13	25	38	25	–
	Sep	3	–	–	33	33	33	–
	Oct	13	–	–	31	46	8	15
	Nov	14	–	29	43	7	7	14
	Dec	24	–	–	4	67	17	13
1997	Jan	2	–	–	–	100	–	–
	Feb	6	83	–	–	–	17	–
	Mar	3	67	–	–	33	–	–

but were absent between August 1995 and January 1996. Very few mice were estimated to be older than twelve months (the oldest mouse being aged at 480 days). Individuals in the last age class were captured in the wet season and the late dry season, but were absent in the late wet season and early dry season (between April and September).

Diet

The stomach contents of *Mastomys natalensis* (n = 57) consisted predominantly of foliage, with seeds and arthropods present at lower frequencies. Seasonal changes in the diet of *M. natalensis* are shown in figure 4. In the dry season (between June and October), the diet of *Mastomys natalensis* consisted entirely of foliage. Seeds were an important component of the diet in the wet months between November and May, while arthropods were part of the diet only in the middle of the wet season between January and April.

Discussion

Reproduction

It has been shown throughout Africa that reproduction in *Mastomys natalensis* is associated with rainfall (COETZEE 1965; TAYLOR and GREEN 1976; NEAL 1977; SWANEPOEL 1980; CHIDUMAYO 1984; BRONNER et al. 1988; LEIRS et al. 1989; PERRIN et al. 1992; WIRMINGHAUS and PERRIN 1993). BRONNER et al. 1988 reported a correlation between rainfall two months previously and reproductive activity in female (but not male) *M. natalensis* from South Africa. A similar correlation was reported by LEIRS and VERHEYEN (1995). The latter study, conducted over several years, included interannual variation in rainfall which, thus, strengthened the observed correlation. In the present study, reproductive activity of

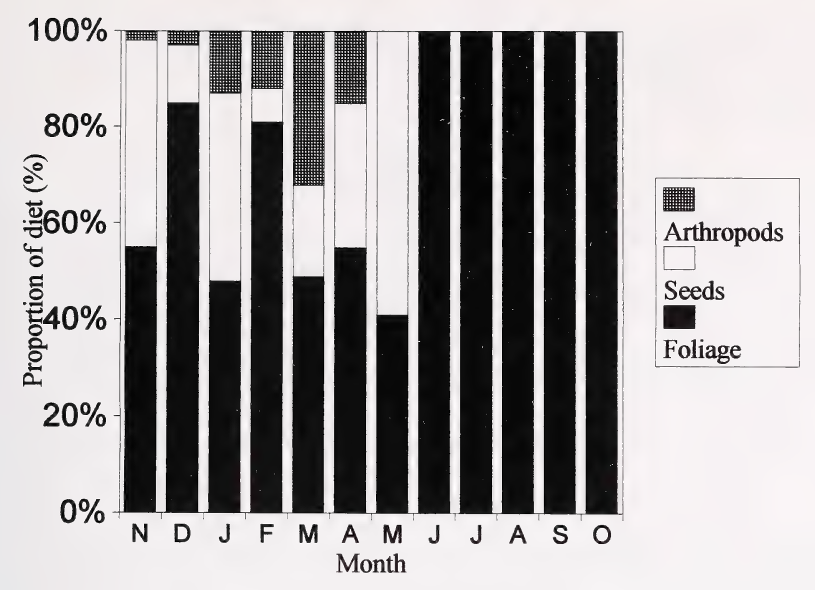


Fig. 4. Seasonal changes in (%) diet composition of *Mastomys natalensis* between November 1996 and October 1997 at eKundizeni Farm, Swaziland.

both male and female *M. natalensis* was correlated with rainfall in the previous month, although the strongest correlation in females was with rainfall two months previously. This supports the suggestion that rainfall is the ultimate factor in the timing of reproduction in female *M. natalensis* (Bronner et al. 1988). In males, in contrast, the strongest correlation was with rainfall in the same month. The reason for this is probably related to the fact that reproductive activity in females was defined by pregnancy, while in males it was defined by scrotal testes. Defined as such, males should be able to respond to rainfall quicker than females.

The litter size of *M. natalensis* reported here (11.4) is very similar to that reported from Morogoro in Tanzania (11.3; Leirs and Verheyen 1995) and that from Zambia (12.4; Chidumayo 1984). There were no differences in litter size between three different age classes of *M. natalensis* supporting the findings of Leirs and Verheyen (1995). Thus, there was no age-specific fecundity. Similar findings have also been reported for *Tatera leucogaster* (Perrin and Swanepoel 1987).

Age structure

The seasonal changes in age structure of *M. natalensis* described in this study are similar to those described in Tanzania (Leirs et al. 1993; Leirs and Verheyen 1995), and to those described by toothwear in South Africa (Coetzee 1965), Uganda (Neal 1977), and Zambia (Chidumayo 1984). *Mastomys natalensis* individuals seldom survive much beyond 12 months, and probably never breed in more than one season. Of the four mice, in this study, whose ages were estimated between 400 and 480 days, one of them was captured in July and probably would not have survived the dry season to breed in a second season. The other three mice were captured in the middle to late wet season and would, thus, have been immatures in the previous breeding season. The older age classes die off at the end of the breeding season (March/April) and are replaced by that season's offspring.

The monthly age structure of this population corresponded with the timing of reproductive activity of the mice and was dissimilar in the two breeding seasons. In the 1995/6

season, pregnant females were first captured in November and immature mice in December. In the 1996/7 season, pregnant females were first captured in December/January and immatures in February.

Diet

Mastomys natalensis exhibits gastro-intetinal and dental characteristics typical of an omnivorous murid rodent (Perrin and Curtis 1980). In this study *M. natalensis* appeared to be omnivorous, feeding on what food was available. In the dry season when seeds and arthropods are present in low numbers (Lack 1986), *M. natalensis* fed only on vegetative plant matter (probably leaves of grasses). In the wet when most grasses seed (van Oudtshoorn 1992) and arthropod numbers increase (Lack 1986), seeds and arthropods contributed up to 50% of the identifiable stomach contents. Similar observations have been made in Tanzania (Leirs et al. 1994; Leirs and Verheyen 1995). In the latter study, the diet of *M. natalensis* was predominantly vegetative plant matter, with arthropod consumption increasing in the wet seasons. Seeds were an important component of the diet during the long "masika" rains when reproduction was at its peak. In Uganda, Field (1975) reported that over 90% of the stomachs of *M. natalensis* contained insect remains which made up 20% of the diet by weight. In Kenya, based on faecal analysis of *M. natalensis*, grass seeds contributed the bulk of food eaten (Oguge 1995). It is likely that seeds and vegetative plant matter are not digested to the same degree (Hansson 1970), and that therefore the results of faecal analysis are skewed toward food material that digests slowly. In Zimbabwe, seeds formed the main component of the diet of *M. natalensis*, while arthropods contributed significantly only in spring and summer (Swanepoel 1980). The latter study was conducted in an agricultural area, and it is thus likely that seeds would have been available throughout the year. In conclusion, it would appear that *M. natalensis* consumes seeds and arthropods when available, but survives on vegetative plant matter throughout the remainder of the year.

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Zusammenfassung

Fortpflanzungsbiologie, Altersstruktur und Nahrung von Mastomys natalensis (Muridae: Rodentia) im Grasland von Swaziland

In einem subtropischen Graslandgebiet in Swaziland wurden der zeitliche Verlauf der Fortpflanzung, monatliche Veränderungen in der Altersstruktur und die Nahrung von *Mastomys natalensis* untersucht. Die Vielzitzenratten wurden jeden Monat über einen Zeitraum von 25 Monaten gefangen. Das individuelle Alter der Tiere wurde mit Hilfe des Augenlinsengewichts geschätzt. Trächtige Weibchen und skrotale Männchen wurden nur in der Regenzeit festgestellt, wobei jahreszeitliche Differenzen im Beginn der Fortpflanzung mit dem Niederschlag korrelierten. Monatliche Veränderungen der Altersstruktur von *M. natalensis* wurden bestimmt durch das Auftauchen von Jungtieren in der Regenzeit und den Tod von fortpflanzungsaktiven Adulten in der folgenden Trockenzeit. Die Mägen von *M. natalensis* enthielten in der Trockenzeit vorwiegend vegetatives Pflanzenmaterial, in der Regenzeit bildeten Samen und Arthropoden einen wesentlichen Anteil.

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Population biology of the subterranean rodent *Ctenomys australis* (Tuco-tuco) in a coastal dunefield in Argentina

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Abstract

The population biology of the subterranean rodent *Ctenomys australis*, tuco-tuco, was studied along a coastal dunefield. Average density was 16.1 ind./ha during the studied period and the animals showed a random spatial distribution pattern. The breeding season lasted the entire year determining a lack of a discrete period of recruitment and a complex age structure. Overall sex ratio was skewed towards females, whereas that for young individuals was even. Females reached sexual maturation before males and brought only one litter to the population in the year they were born. During summer, females showed overlap between pregnancy and lactation demonstrating the existence of a post partum estrus. Mean litter size was 2.9, in which litter size from post partum estrus was lower than that corresponding to the first pregnancy. Adult animals were sexually dimorphic both in weight and length. Males presented low relative testes length. Dispersal happened above-ground. Mean monthly recovery percentage was 19%. Group of colonizers was composed predominantly by immature animals. No differences were found concerning sex ratio, age structure, and litter size between dispersers and residents.

Key words: *Ctenomys australis*, population biology, dispersal, subterranean rodents

Introduction

The distribution of *Ctenomys* rodents covers a large area of South America, extending from 17 °S to 54 °S latitude and from the Andes to the Atlantic Ocean. Within this area they occur in a wide variety of habitats. This habitat versatility is indeed a reflection of the subterranean way of life, as the permanent plugged burrows insure microclimatic conditions of both humidity and temperature relatively independent of the exterior ambient conditions (ROSENMANN 1959). Nonetheless, a more detailed study of their distribution showed that tuco-tucos are prone to live in sandy soils or at least in well-drained ones (CONTRERAS 1973). This is not only due to digging but to metabolic constraints related to heat storage and respiratory gas exchange (MCNAB 1966). As a consequence of its size, *C. australis* occupies looser, more friable soils than smaller species (VLECK 1979; BUSCH 1989; CONTRERAS and MCNAB 1990). This fact conditioned their distribution, which is restricted to the southern coastal region of Buenos Aires province from Necochea to Bahia Blanca in a sandy dunebelt close to the beach.

C. australis shows individual territoriality. They perform most of their dairy activities in permanently sealed burrow systems, making only brief surface excursions for collecting

plant material. Thus, the burrow system plus a narrow surface periphery compose the exclusive territory for each individual. This particular way of life coupled to little success with rearing individuals of this species under conditions of captivity, make it difficult to obtain ecological data.

The aim of the present study is to provide information about life history traits on one species dwelling underground. This will be useful in terms of finding possible interpretations for the extraordinary specific diversification undergone by this genus (Reig et al. 1990) in contrast to what is found in other genera that share the same way of life. Furthermore, since *C. australis* is restricted to natural grasslands over sand dunes, which are considered as vulnerable habitats, this rodent warrants special conservation status for which knowledge of its biology would be useful.

Material and methods

Study area

The study was conducted 10 km south of Necochea, Buenos Aires, Argentina. It consists of a 4–10 km wide coastal dune fringe which slopes into the inland natural grassland. Sand dunes reach altitudes ranging from 30 to 50 m above sea level, and extend 200 to 2 000 m (Frenguelli 1928). The natural grassland over the dunes exhibits a vegetation cover of about 20%, with dominant plants including *Poa* sp., *Panicum racemosum*, and *Calistelgia soldanella* (Malizia et al. 1991).

Data collection and analysis

Individuals of *C. australis* were collected in six trapping periods from May 1991 to May 1992. In each sampling period, which extended over 5 days, the capture area was placed along a coastal dune fringe nearly 1 km far away from that corresponding to the previous ones. Such an arrangement was chosen both not to perturb the population and to minimize the effect of producing vacant areas in our results. The fact that *C. australis* individuals restrain their activities to their burrow system and are highly sensitive to handling, makes it extremely difficult to implement mark-recapture programs. This situation led us to implement a removal method. To perform the trappings, snap-traps Oneida Victor N° 0 (without any kind of bait) were located at the entrance of the burrows to catch all individuals present in each removal area which averaged 0.80 ha in size (range 0.50–1.25 ha). Edge effects leading to possible counting errors were eliminated by considering exclusively the individuals that have all the tunnel openings (commonly used for foraging activities) inside the removal area. The traps were checked hourly during daylight hours and closed during the night. Position of capture was recorded to determine spatial distribution. In spite of the recognized limitations of data coming from removal of all animals occupying an area, it constitutes the only way to obtain ecological information for this species. On the other hand, this methodology allows to obtain detailed information of the reproductive status of individuals.

Body weights and linear measurements were taken at death and reproductive condition was obtained by autopsy. Immature females were characterized by presence of filiform uterus, closed vagina, and no follicular activity whereas subadult females presented follicular activity. Reproductive individuals showed an open or plugged vagina, ripe follicles, placental scars, signs of pregnancy or postpartum pregnancy. Males with spermatozoa in epididymis were classified as mature. Ossification of humeri was used to determine six relative age classes. All reproductive and age criteria were taken from Pearson et al. (1968) and Malizia and Busch (1990). These data provided information about density, spatial distribution pattern, reproductive activity, and age structure of the resident population.

To assess dispersion of *C. australis*, two experimental plots 3 km apart, one 1.44 ha (S plot) and another 0.77 ha (N plot) were delimited and all the tuco-tucos present inside the plots were removed. No mound building activities were detected once removal was concluded. Individuals that subsequently colonized these previously vacated areas were removed from July 1992 to May 1993 (S plot) and from September 1992 to May 1993 (N plot). These individuals were considered as dispersers in this study. Those individuals living close to the edges of the experimental plots that could have moved underground simply by extending their burrow systems were not included in our analysis. We easily recog-

nized them since they were initially marked. Dispersal individuals were autopsied and the same data registered as for residents.

Results are given as X ± SE. The T-square distance method was used to analyse the spatial pattern of populations found continuously across the grassland (LUDWIG and REYNOLDS 1988). Chi-square tests were used to determine whether sex ratio deviated from parity. Non parametric Kruskall-Wallis tests were used to compare differences between litter size from first and second pregnancy and between residents and dispersers. Differences in body mass and length between males and females were tested using t-test. Chi-square contingency table analysis was used to test independence between sex and condition of animals (residents or dispersers); similarly was tested whether relative frequencies of animals of each reproductive condition were the same for residents and dispersers.

Results

Density and spatial distribution

Average density was 16.1 ± 1.1 ind./ha during the study period. Densities in samples were 20 ind./ha (May/1991), 17.2 ind./ha (August), 10 ind./ha (October), 14.4 ind./ha (December), 26.7 (March/1992), 8.0 ind./ha (May), 10.0 ind./ha (July). These records come from removal areas of 0.80 ha average in size (range 0.5–1.25 ha). In computing densities, juvenile individuals sharing the maternal burrow were not considered, whereas non captured individuals which presented clearly mound-building activity were scored.

Indices derived from distances between points and individuals in arbitrary sampling units were used for spatial pattern analysis. Table 1 shows average distances between points and individuals and spatial patterning indexes for each sampling period. The distribution of *C. australis* was random. Both z values for Spatial Pattern Index (C) and Johnson and Zimmer Index of Dispersion (I; LUDWIG and REYNOLDS 1988) were lower than the critical values for each sampling period. Thus, we accepted the hypothesis that the distances were measured between points and individuals within an underlying random pattern.

Table 1. Mean distance between individuals and random points used to calculate spatial patterning indexes for *Ctenomys australis* from Necochea.

	Sample					
Mean distance (m)	May	Aug	Oct	Dec	Mar	May
Point-nearest individual	13.3	11.25	22.24	13.06	12.76	20.69
Individual-nearest neighbor	18.53	21.76	41.06	29.28	16.45	37.16
Spatial pattern Index (C)	0.49	0.40	0.52	0.43	0.58	0.40
z statistic	–0.15	–1.83	0.30	–1.34	1.54	–1.86
Dispersion Index (I)	2.30	2.18	2.11	1.72	1.76	1.85
z statistic	0.92	0.55	0.32	–0.85	–0.72	–0.45

z (crit) = 1.96 P = 0.05

Sex ratio

Since numbers from each sample were in general too small to perform valid statistical tests, the data were grouped and tested for overall differences.

The sex ratio of younger individuals (relative age class i, n = 26) was nearly even (1 male: 0.75 female; $X^2 = 0.57$, df = 1, P > 0.05) but the adult sex ratio (n = 50) was heavily skewed toward females (1 male: 2.125 females; $X^2 = 6.48$, df = 1, P = 0.011).

Age and maturation

To characterize the individuals belonging to the six relative age classes that resulted by ranking the epiphyseal ossification of humeri, data provided by autopsy plus that obtained from animals reared in captivity were used.

Individuals belonging to age class i were captured at the same location as the mother or close to her. For this reason they were not considered as residents. Mean body weight was 119.3 ± 38.7 g and 118.1 ± 28.3 g for males and females, respectively. These animals can be attributed to a chronologic age of 0 to 3 months. Smaller individuals of this group were sucklings.

Those individuals of age class ii were captured in their own tunnel system. All males had no spermatozoa in their epididymis and their mean body weight was 236 ± 74.4 g. Females had experienced follicular activity and a mean body weight of 216 ± 49.6 g. We estimated a chronologic age around 3 to 6 months for this group.

Males of age class iii (mean body weight = 264.9 ± 5.9 g) were all mature and most of the females (mean body weight = 261.7 ± 58.1 g) presented signs of pregnancy; all were between 6 to 9 months old.

At age class iv, the mean body weight was 327.1 ± 62.7 g and 268 ± 48.5 g for males and females, respectively. Females were pregnant or showed signs of previous pregnancies. The age of these animals was estimated to be 9 to 12 months.

Males of age class v weighted 330 ± 93.2 g and females 324 ± 38.5 g. Males from age class vi showed no evidences of senility since all of them presented spermatozoa in their epididymis (mean body weight = 416.5 ± 54.3 g). The only female captured belonging to this age class weighted 334 g. For the two later age classes no chronologic age could be assigned.

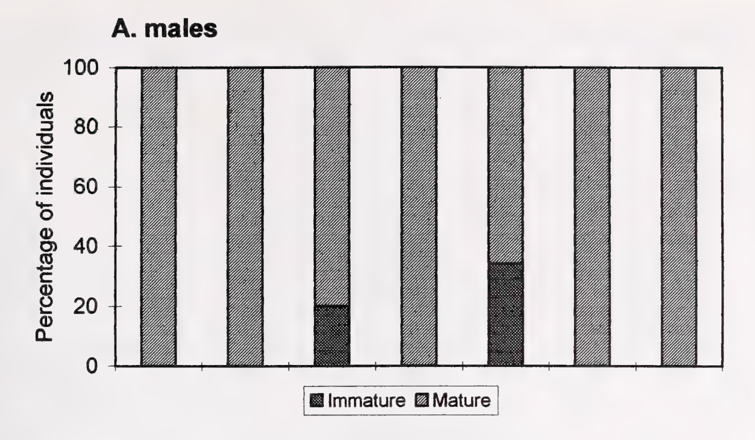
Reproduction

Considering the breeding period as the time during which females are pregnant, it can be inferred that *C. australis* has a continuous one. Once sexual maturation is attained in either sex, the animal remains in reproductive activity for the entire year round (Figs. 1 a, b). Pregnant females were scored throughout the entire year and since they attain maturity nearly at six months of age, they brought only one litter to the population in the year they were born. During summer (December and March samples) females showed overlapping between pregnancy and lactation, evidencing the existence of a post partum estrous.

For *C. australis*, information concerning longevity and length of gestation period is unavailable, nonetheless we can estimate that the females could produce three or four litters in their life span considering that for *C. talarum* these values were calculated as 2 years and 102 days, respectively (Busch et al. 1989; Weir 1974).

Litter size

Mean litter size (determined by embryo counts, which could slightly overestimate litter size at birth) was 2.9 ± 1.37 ($n = 20$). Nonetheless, if we compare the litter size from the first and second pregnancies (the last one produced as a result of a post partum estrous), we found an interesting difference. The second litter was smaller than the first one (1.85 ± 1.07, $n = 7$ and 3.46 ± 1.19, $n = 13$, respectively; $U_{crit} = 76.5$, $df = 1$, $P < 0.01$). Furthermore, females both during lactation and pregnancy showed a high incidence of pre- and postimplantation embryo losses, as evidenced both from no matching between number of corpora lutea and embryos and clear resorbtion of embryos.



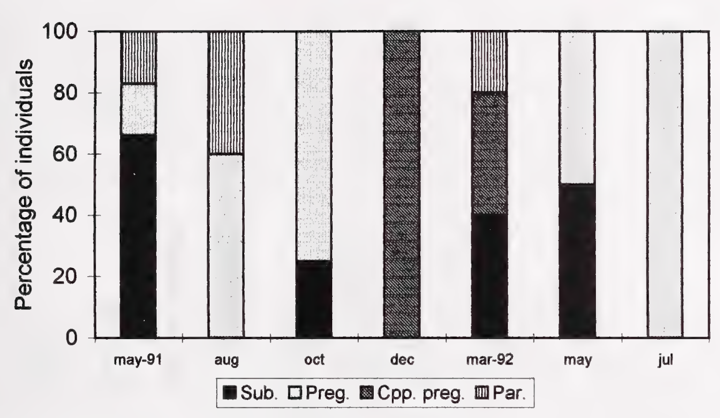


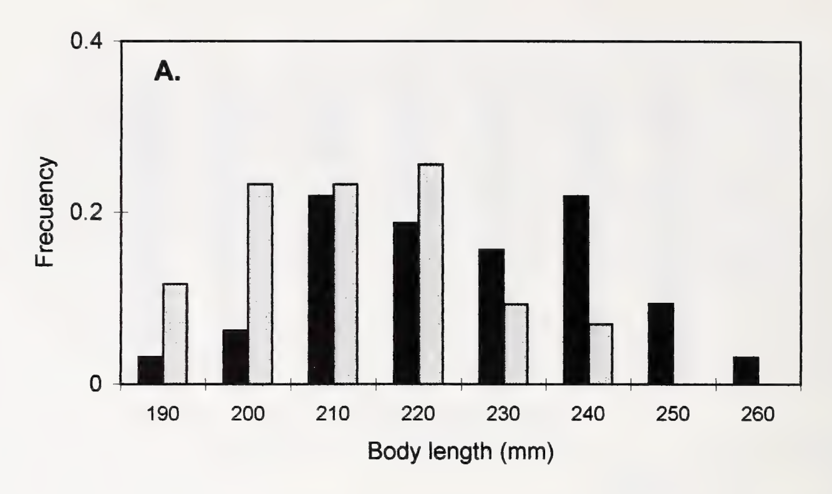
Fig. 1 a) Proportion of mature and immature male individuals of *Ctenomys australis*; b) Proportion of reproductive (par = parous, cpp. preg. = pregnant and lactating, preg = pregnant) and non-reproductive (sub. = subadult, imm = immature) female individuals of *Ctenomys australis*.

Sexual size dimorphism and relative testes size

Adult individuals of *C. australis* show a clear sexual size dimorphism, i.e. males being larger than females. Frequency distribution analysis (Fig. 2) and male: female ratio indicate the existence of a more pronounced dimorphism in mass than in length. Ratio of dimorphism in weight was 1.3 with a mean weight of 367 ± 69.2 g ($n = 32$) for males and 288 ± 50.1 g ($n = 43$) for females ($t = 5.64$, $P < 0.01$), while the ratio in length was 1.1 and mean length of 221 ± 15.1 mm ($n = 32$) for males and 206 ± 12.9 mm ($n = 43$) for females ($t = 4.28$, $P < 0.01$). Relative testes size (testis/body length) was 0.054 ± 0.007 ($n = 30$).

Dispersal

During the study period, 54 individuals colonized previously vacated areas by aboveground (30 animals for S plot and 24 for N plot). Both areas remained without animals at the first sampling period, showing with certainty that all the tucos had been effectively removed. Subsequent occupation was performed using old tunnel systems, as evidenced by location of the animals in the field.



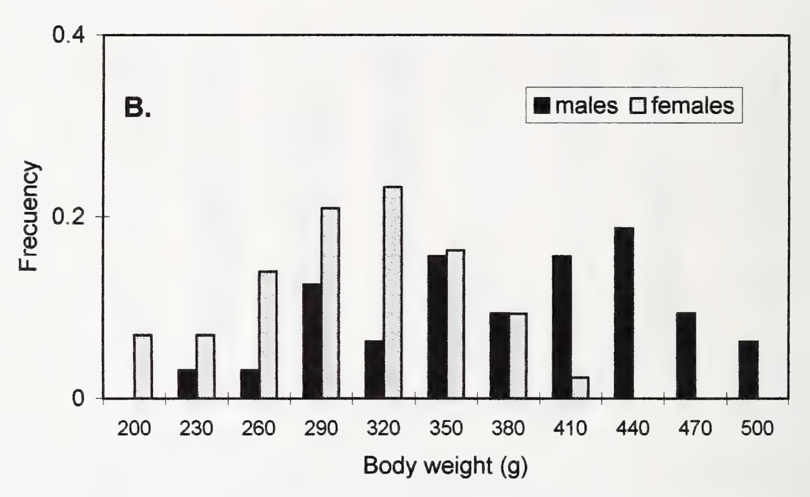


Fig. 2. Frequency distribution of body length (A) and body weight (B) of *Ctenomys australis*.

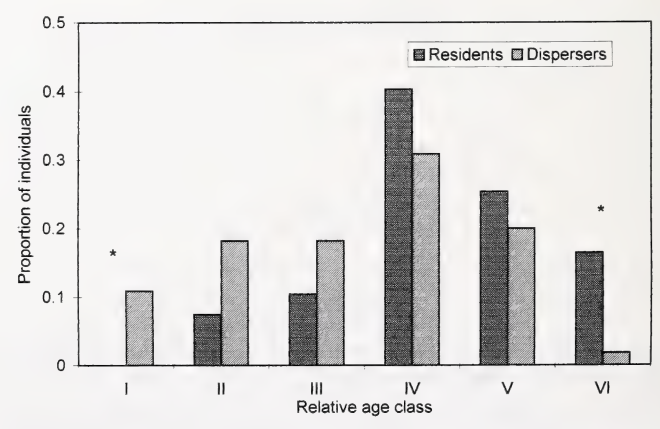


Fig. 3. Proportion of resident and disperser individuals of *Ctenomys australis* (both sexes pooled) for each relative age class.

Mean monthly recovery percentage (number of colonizers removed from the experimental plot at time t/resident population size at the same time × 100) was 10.8% (range 0–20%) for the S plot and 27.0% (range 0–65%) for the N plot, with a general average around 19%.

Due to sample size, we pooled data coming from the two experimental plots in the analysis of residents versus dispersers. The group of colonizers was composed by the same proportion of both sexes (1 male: 1.25 female, $X^2 = 0.66$, df = 1, P = 0.417). Although the resident population showed a clear skew towards females, dispersers and residents did not differ significantly ($X^2 = 1.69$, df = 1, P = 0.194).

Reproductive activity and dispersal proved to be dependent attributes for both sexes (females: $X^2 = 5.19$, df = 1, P = 0.023; males: $X^2 = 7.18$, df = 1, P = 0.007). Representation of reproductive individuals was higher for male and female resident population than for dispersers. Resident males were mostly reproductive (90.8%, n = 21), whereas for dispersers this proportion was only 54% (n = 24). Likewise, reproductive females represented 75% (n = 40) for residents and 48.4% (n = 29) for dispersers. In addition, 40% of non-reproductive female dispersers were subadults with follicular activity. Pregnant females also dispersed. Their mean embryo counts were 3.7 ± 0.63 (n = 13) and did not differ from that belonging to general mean litter size and first pregnancy for residents (U = 99, P = 0.23 and U = 81, P = 0.84, respectively).

The age composition of dispersers did not differ significantly from that of residents. Comparisons of the percentage of dispersers versus that of the residents for each relative age class showed that only the extremes of the age distribution differed (Fig. 3). We found no resident individuals of age class i and few animals of age class vi participating in the dispersal process ($z_{obs} = 3.7$ and 3.09 respectively, $z_{crit} = 1.96$, $P < 0.05$).

Discussion

In contrast to voles, the mammalian r-strategist par excellence, which possess a high capacity to expand their numbers in transient habitats and produce large litters during gestation periods comprising few weeks by early reproductive females, *C. australis* as other *Ctenomys* populations is a relatively K-selected group of rodents. They breed later, develop slower, are more stable in numbers and have fewer offsprings than voles.

Random distribution pattern for *C. australis* found in this study may be a consequence of both population densities under carrying capacity and habitat characteristics, since coastal sand dunes are ecologically homogeneous habitats determining no concentration of animals in propitious patches. In contrast, uniform dispersion patterns were reported for other *Ctenomys* populations under high density conditions as well as in poor habitats (Pearson et al. 1968; Gallardo and Anrique 1991; Rosi et al. 1992), whereas clumped distribution has been showed for *C. talarum* populations occupying grasslands with high plant biomass (Malizia 1994). Hansen and Remmenga (1961) have found displacements from clumped to uniform patterns in *Thomomys talpoides* with density increases.

The significant change in male to female ratio that occurs between new-born and adult *C. australis* indicates different mortality rates among sexes. Sex ratio skewed toward females suggests that this population is polygynous such that male-male aggression may play an important role in determining successful territory defense and access to multiple females.

Another source of mortality has been analysed for *C. australis*. Vasallo et al. (1994) found that only subadults were preyed upon by owls but the authors could not distinguish differences between sexes since no valid discrimination was obtained from pellet information. Thus, predation is more common than previously assumed for *Ctenomys* species although we have no information whether their incidence is uneven among sexes.

The studied population showed sexual bimaturism, females being the first to attain reproductive potentiality. An association between the degree of polygyny of a species' mating system and the extent to which males mature later than females has been reported (DALY and WILSON 1983). Since polygyny enhances male-male competition, it seems possible to interpret delayed maturity as a response to that competition.

Evidence for polygyny is reinforced from other sources. EMLEN and ORING (1977) predicted that in breeding systems where one male has exclusive access to multiple females, selection should cause the existence of sexual dimorphism in size. The more pronounced dimorphism in body weight than in length for *C. australis* may be attributed to the interplay between sexual and growth hormones leading to more robust males in comparison with females of similar length (BOONSTRA et al. 1993). Furthermore, a strong correlation exists between testes size and mating systems since its size is a consequence of copulatory frequency (SHORT 1977). Relative testes length found in this study for *C. australis* is still lower than the mean value reported for polygynous voles by HESKE and OSTFELD (1990). Thus, adult sex ratios skewed toward females (which could be considered an approximation of the operational sex ratio), sexual bimaturism, sexual size dimorphism both in weight and in length, and small relative testes size are all measures that allow to consider the studied population of *C. australis* as polygynous.

Since in *C. australis* the breeding season is continuous, it appears that photoperiod is not the cue that determines breeding in this species. For a subterranean rodent, composition and cover of plants would be a more reliable variable than photoperiod. In this sense, a detailed study on dietary preferences of *C. talarum* and *C. australis* (COMPARATORE et al. 1995) has revealed that *C. australis* is a herbivorous generalist feeding principally on the aerial fraction of vegetation with biomass in the grassland not differing between seasons.

Up to date, no information about production of secondary compounds from growing plants is known to stimulate reproduction in *Ctenomys* as was described for other rodents (ROWSEMITT and O'CONNOR 1989).

Continuous breeding determines the lack of a discrete period of recruitment as well as a complex age structure. This reproductive adaptation allows that more individuals were able to participate in matings, even young of the year, thereby moderating the potential effects of genetic drift that operates in populations where reproduction is over a short period.

Mean litter size of 2.9 reported here for *C. australis* is 30% lower than for *C. talarum* at two different localities (MALIZIA 1994). This situation could be related to grassland quality since plant cover where *C. talarum* inhabits is up to 80%. On the other hand, *C. mendocinus* (ROSI et al. 1992) shows the same litter size as *C. australis* and is distributed in xeric habitats with poor plant cover. Lower mean embryo counts for post partum pregnancies may be attributed to maternal care of the first litter, which limits the time and energy dispensability of the mother to collect plant material in a poor habitat, such as a sand dune.

Few studies exist dealing with direct quantification and characterization of dispersal of subterranean rodents (WILLIAMS and CAMERON 1984; RADO et al. 1992; MALIZIA et al. 1995; O'RIAIN et al. 1996). Nonetheless, more information has been provided by other authors which examined inferentially movements in this group of rodents (HOWARD and CHILDS 1959; VAUGHAN 1962; WILKS 1963; SMOLEN et al. 1980; PEARSON et al. 1968).

Recovery percentages reported here are nearly in the order of that found for *C. talarum* (MALIZIA et al. 1995) and *Geomys attwateri* (WILLIAMS and CAMERON 1984) and compares favorably only with the microtine *Microtus pennsylvanicus* (TAMARIN 1977) which presented the lowest dispersal rate among surface-dwelling rodents. This reflects an expected situation where low vagility appears associated with high local dependence of subterranean rodents to their local habitat.

Although male dispersal is proposed as a rule for mammals (Greenwood 1980), this pattern is not clear for subterranean rodents. Both sexes of *C. australis*, *G. attwateri*, and *C. talarum* from Necochea locality dispersed, whereas *C. talarum* from Mar de Cobo locality showed a predominance of males dispersing. This is a confusing result for *C. australis*, since the proposed polygyny may be associated with male dispersal. It is possible that the breeding system, mediated by the access to multiple females, would be responsible for dispersal of one part of the population (males), whereas for females, another source of resources, such as space, may be responsible for their mobility.

Previous experimental and inferential studies examining pocket gopher dispersal revealed that dispersers were usually young individuals. This situation fits the optimal dispersal theory for subterranean rodents (Nevo 1979, 1982) which predicts that once adults have established their territories, they will remain sedentary throughout their lives. This is not the case for *C. australis* in which, in spite of the absence of oldest individuals dispersing, the age structure of this group was a random sample of the resident population. Nonetheless, this dispersing group is characterized by being predominantly non-breeding individuals. The same trend was found for *C. talarum* (Malizia et al. 1995).

This characterization shows that dispersers are individuals leaving their natal site driven by the lack of resources that insure successful reproduction.

The fact that one part of the population disperses before reproduction has been proposed as a mechanism for avoiding inbreeding (Dobson 1982).

Apfelbaum et al. (1991) found moderate levels of genetic heterogeneity among four analysed populations of *C. australis*, where gene flow appears to play a significant role only in allowing the maintenance of a slight local differentiation. The ecological mechanisms that promote such a situation may be associated with the levels of vagility found in this study, coupled to both a random distribution pattern of individuals in a homogeneous habitat and the existence of a long breeding season. This determines both the lack of a discrete period of recruitment and the ability of more individuals participating in the reproductive process. All these factors contribute to make *C. australis* population relatively stable. In this sense, the persistence of these populations may depend strongly on the availability of propitious habitats according to its energetic and thermoregulatory restrictions. A previous study (Zenuto and Busch 1995) has demonstrated that *C. australis* mound-building and feeding activities maintain suitable habitats for themselves. Thus, it is important to control human land use in such a manner to guarantee the persistence of this special and vulnerable habitats.

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Zusammenfassung

Populationsbiologie des unterirdisch lebenden Nagers Ctenomys australis (Tuco-tuco) in einem Dünenfeld an der Küste von Argentinien.

Die Populationsbiologie des unterirdisch lebenden Nagers *Ctenomys australis* (Tuco-tuco), wurde entlang eines Küstendünengebiets studiert. Die mittlere Populationsdichte lag in der beobachteten Periode bei 16.1 Ind./ha, wobei die Tiere eine zufällige räumliche Verteilung zeigten. Die Fortpflanzung erfolgte ganzjährig, was das Fehlen einer fest definierten Wurfperiode sowie eine komplexe Altersstruktur der Population bedingte. Das Geschlechterverhältnis war, bezogen auf die Gesamtpopulation,

zu den Weibchen hin verschoben, während es bei den Jungtieren ausgeglichen war. Weibchen erreichten die Geschlechtsreife früher als die Männchen, hatten im Jahr ihrer Geburt aber nur einen Wurf. Im Sommer war bei den Weibchen eine Überlappung von Schwangerschaft und Laktation zu beobachten, wodurch die Existenz eines Postpartum Oestrus belegt wird. Die mittlere Wurfgröße betrug 2.9 Jungtiere, lag aber beim Postpartum Oestrus niedriger als bei der ersten Schwangerschaft. Die adulten Tiere zeigten einen Geschlechtsdimorphismus hinsichtlich Gewicht und Größe. Bei den Männchen war eine geringe relative Hodengröße zu beobachten. Dispersionen fanden, trotz überwiegend unterirdischer Lebensweise, oberirdisch statt. Die monatliche Ersetzungsrate lag bei 19%, wobei die Besiedlergruppe überwiegend aus nichtgeschlechtsreifen Tieren bestand. Zwischen Besiedlern und residierenden Tieren konnten keine Unterschiede hinsichtlich Geschlechterverhältnis, Alterszusammensetzung und Wurfgröße festgestellt werden.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Funktionelle Asymmetrie bei Katzen

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Rechtshändigkeit verbunden mit Hemisphärenspezialisierung für Sprache wird im allgemeinen als ein markantes Merkmal des Menschen bezeichnet (Bourassa et al. 1996; Elliott et al. 1996; Iaccino 1993; Reiss 1991). Hierbei besitzt die manuelle Spezialisierung eine große Bedeutung in Bezug auf Cognition und phylogenetische Herausbildung des typischen menschlichen Verhaltens (Bradshaw et al. 1993).

In den letzten Jahrzehnten wurde jedoch der Seitendominanz bei Tieren wieder zunehmende Beachtung geschenkt. Morphologische Asymmetrien konnten insbesondere bei wirbellosen Tieren beobachtet werden (Bianki 1993; Elliott et al. 1996). Neben der Hemisphärenspezialisierung selber wurde auch die funktionelle Asymmetrie der Gliedmaßen untersucht. Hierbei ist das Hauptaugenmerk besonders auf nichthumane Primaten gerichtet worden (Bianki 1993; Bradshaw et al. 1993; Iaccino 1993). Allerdings existieren nur wenige Angaben über die funktionellen Asymmetrien bei Katzen. Dagegen scheint gerade die Katze ein guter Kandidat für solche Untersuchungen zu sein, da sie über eine gewisse manuelle Geschicklichkeit der vorderen Extremitäten verfügt (Bianki 1993; Iaccino 1993).

Noch 1968 bemerkte Poeck (1968), daß die Katze, das klassische Tier in der Neuropsychologie, sowohl morphologisch als auch funktionell ein symmetrisches Gehirn aufweist. Andere Autoren konnten dagegen später zeigen, daß doch Rechts-Links-Differenzen bestehen (vgl. Mascetti 1997). Während die meisten Autoren berichteten, daß Katzen eine individuelle Seitendominanz besitzen (Cole 1955; Forward et al. 1962; Tan et al. 1990; Warren et al. 1967), ist nicht klar, ob in den Populationen eine signifikante funktionelle Asymmetrie ähnlich der Rechtshändigkeit beim Menschen existiert (Bianki 1993; Bourassa et al. 1996; Forward et al. 1952; Ward et al. 1993). Einige Studien konnten eine nichtsignifikante Überlegenheit der linken Seite zeigen (Cole 1955; Forward et al. 1962), während andere eine signifikante linksseitige Dominanz nachweisen konnten (Fabre Thorpe et al. 1993). Tan und Mitarbeiter (Tan 1993; Tan et al. 1991) meinten, daß die von ihnen gefundenen Asymmetrien bei Katzen abhängig vom Geschlecht seien. Neun der untersuchten männlichen Katzen waren linksdominant und 13 Katzen rechtsdominant (Tan 1993). Es besteht bei weiblichen Katzen ein Überwiegen der Rechtsdominanz, die auch bei anderen Tieren und Menschen beobachtet wird (Bianki 1993; Bradshaw et al. 1993; Ward et al. 1993). Die Häufigkeit der Katzen ohne Dominanz wird in der Literatur mit 12% bis 50% angegeben (Cole 1955; Forward et al. 1962; Warren et al. 1967). Bei den meisten bisher getesteten Katzen handelt es sich nicht um freilebende

Katzen, sondern um Labortiere. Das Ziel der vorliegenden Studie ist es, eigene Daten über die Händigkeit von freilebenden Katzen vorzulegen, wobei auch Geschlechtsunterschiede berücksichtigt werden.

In den Jahren 1989 bis 1997 konnten insgesamt 41 Katzen (*Felis silvestrius* f. catus) beobachtet und untersucht werden. Es handelt sich um 20 männliche und 21 weibliche Katzen. Die Tiere leben überwiegend in einem Freigelände (Margaretenhof in Reick – Dresden), wobei die Zahl im Untersuchungszeitraum wechselte. Die Tests erfolgten fast ausnahmslos in den Abendstunden. In der Literatur werden verschiedene Methoden zur Bestimmung der Händigkeit bei Katzen angegeben. Das einfache Zureichen von Futter erschien uns hierbei nicht als geeignete Methode. Oftmals wurde nämlich dabei das Futter nicht mit der Pfote, sondern mit dem Maul „erlangt". Den Katzen wurde deshalb ein Futterstück angeboten, welches sich auf einem Podest von 20 cm befand. Der Zugriff war durch eine gitterartige Barriere erschwert, so daß die Katzen das Futterstück nur mit den Pfoten erreichen konnten.

Es wurden insgesamt 10 Testserien pro Individuum an verschiedenen Tagen durchgeführt, wobei der Zeitraum zwischen den Untersuchungen nicht größer als vier Tage betrug. Eine Serie umfaßte 6 Versuche. Wurde nur viermal eine Seitenkonstanz registriert, wurden noch einmal drei Versuche durchgeführt. Zeigte sich dann insgesamt nur eine Seitenkonstanz bei 4 oder 5 von insgesamt 9 Versuchen, wurde das Ergebnis als symmetrisch bzw. beidpfotig eingestuft. Eine Dominanz lag vor, wenn die Katzen bei 5 bzw. 6 (bei 6 Versuchen) oder 6 bis 9 (bei 9 Versuchen) Testproben eine Seitenkonstanz aufwiesen. Die entsprechende gesamte Rechtsausführung wurde mit +1 und die Linksausführung mit –1 bewertet. Die „Gesamtdominanz" wurde unter Berücksichtigung aller 10 Serien mittels Addition errechnet. Es resultiert eine Wertungsstrecke von +10 (ausgeprägte Rechtsdominanz) bis –10 (ausgeprägte Linksdominanz). Unter Berücksichtigung einer symmetrischen Kategorienbildung wurden drei Dominanzgruppen definiert: Rechtsdominanz (+10 bis +4), Linksdominanz (–4 bis –10) und Symmetrie (+3 bis –3).

In den 10 durchgeführten Testserien konnte insgesamt eine hohe Seitenkonstanz nachgewiesen werden. Die einzelnen Tests ergaben bei keiner Katze eine Symmetrie, d. h. alle der insgesamt 410 Testserien demonstrierten nach dem erwähnten Kriterium eine Seitenbevorzugung. Die daraus abzuleitende „Gesamtdominanz" entsprechend der o. g. Kriterien zeigt die Tabelle 1. 24 der insgesamt 41 Katzen waren rechtsdominant, 11 linksdominant und nur sechs Katzen zeigten keine Seitenbevorzugung. Die Geschlechtsunterschiede sind statistisch nicht signifikant ($chi^2 = 1{,}46$, FG = 2). In der Abbildung 1 ist die Verteilung der manuellen Dominanz in graphischer Form dargestellt. Bemerkenswert ist, daß keine Katze den Punktwert +10 oder –10 aufwies. Diese Punktwerte würden einer ausgeprägten Seitenstetigkeit entsprechen.

Untersucht man die funktionelle Asymmetrie bei bestimmten Probandenkollektiven oder Tiergruppen, so kann man eine individuelle von einer Populationsasymmetrie unterscheiden (Bianki 1993; Bradshaw et al. 1993; Iaccino 1993; Reiss 1991). Die überwiegende Mehrzahl der Menschen sind konstant Rechts- oder Linkshänder. Die meisten Menschen sind rechtshändig, und nur etwa 8% weisen Linkshändigkeit auf (Bourassa et

Tabelle 1. Verteilung der funktionellen Asymmetrie bei 41 Katzen. Aufschlüsselung nach den drei Dominanzgruppen und nach dem Geschlecht. Prozentuale Verteilung in Klammern.

	männlich und weiblich		männlich		weiblich	
Rechtsdominanz	24	(58,6)	10	(50,0)	14	(66,7)
Symmetrie	6	(14,6)	3	(15,0)	3	(14,3)
Linksdominanz	11	(26,8)	7	(35,0)	4	(19,0)

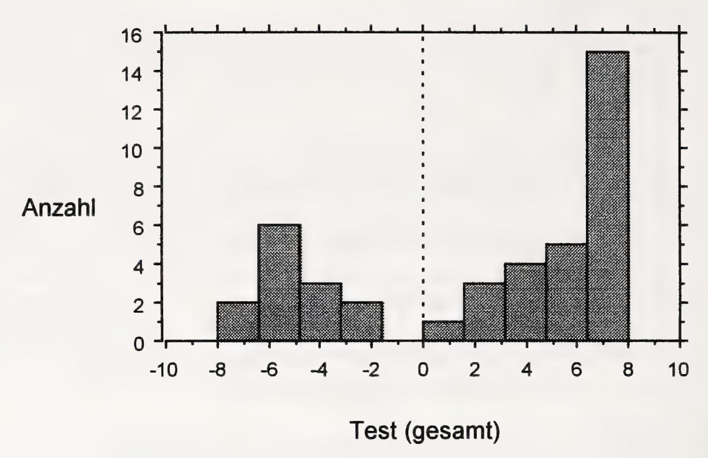


Abb. 1. Verteilung der funktionellen Asymmetrie bei 41 Katzen. Im Gegensatz zur Tabelle 1 wurde die Seitenstetigkeit berücksichtigt. Abszisse: Grad der manuellen Dominanz errechnet aus den 10 Tests (Test gesamt) = Wertungsstrecke von +10 (ausgeprägte Rechtsdominanz) bis –10 (ausgeprägte Linksdominanz). Ordinate: Anzahl der Katzen

al. 1996). Bei Tieren besteht darüber keine Einstimmigkeit. Es wurde sogar postuliert, daß Tiere weder eine Individual- noch eine Populationsasymmetrie aufweisen (vgl. Poeck 1968). Gerade bei Katzen wurden, im Gegensatz zu Mäusen, Ratten, Gorillas oder Hunden, die häufig untersucht wurden, und bei denen eine gewisse Populationsasymmetrie nachgewiesen werden konnte (Bianki 1993; Elliott et al. 1996), bisher nur wenig Untersuchungen vorgelegt. Allerdings konnte bei Katzen eine hohe individuell konstante Bevorzugung einer Seite nachgewiesen werden (Warren et al. 1967).

Neben Art der Erfassung der manuellen Dominanz spielt auch das Auswertungsverfahren eine Rolle. Wie beim Menschen ergibt die Summe mehrerer Testaufgaben eine Skala, auf der dann die Rechts-, Links- bzw. Beidhändigkeit abgegrenzt wird. Da in der Regel ein objektives Kriterium fehlt, ist die Differenzierung mitunter etwas willkürlich, und die Händigkeitsverteilung differiert dann auch entsprechend (Bourassa et al. 1996; Reiss 1991).

Nur wenige Autoren berücksichtigten das Geschlecht. Unsere Studie konnte keine Unterschiede feststellen, obwohl andere Autoren beispielsweise eine Rechtsdominanz bei weiblichen Tieren nachwiesen (Elliott et al. 1996; Tan 1993).

Unsere Ergebnisse zeigen, daß eine funktionelle Asymmetrie bei Katzen existiert, wobei nicht nur eine Individualasymmetrie, sondern Populationsasymmetrie zu beobachten ist. Auffallend ist die zweigipflige oder bimodale Häufigkeitsverteilung (Bianki 1993; Iaccino 1993). Eine dem Menschen entsprechende starke Dominanz (Bourassa et al. 1996) besteht jedoch nicht.

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Camelus thomasi Pomel, 1893, a possible ancestor of the one-humped camel?

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Members of the order Tylopoda are accepted to be emigrants from the western to the eastern hemisphere via the Bering Land Bridge (THENIUS 1972). The time of their arrival in the Old World cannot be established exactly, but the earliest fossil remains of camelids from Asia date to the Middle Pliocene (KOZHAMKULOVA 1986). From the fossil record it is clear that the Plio-Pleistocene witnessed the presence of several species in the Palaearctic region. At least one camelid species is known from Africa as early as the Upper Pliocene (HOWELL et al. 1969; GENTRY and GENTRY 1969).

Fossil camels of the genus *Camelus* Linnaeus, 1758 descend from Plio-Pleistocene forms of the genus *Paracamelus* Schlosser, 1903, recorded from localities in north-eastern China, north-western Mongolia, Tadzhikistan, and Kazakhstan (KOZHAMKULOVA 1986). Toward the end of the Pleistocene, the genus *Camelus* already had disappeared from large parts of its former Eurasian distribution area. Though population numbers of Old World camelids continued to decline, it is a fact that in the course of the Holocene two domestic forms make their appearance, for which LINNAEUS (1758) proposed the names *Camelus dromedarius* Linnaeus, 1758 and *Camelus bactrianus* Linnaeus, 1758 to designate respectively the one-humped and the two-humped form. The wild ancestor of the latter, first described by PRZEWALSKI in 1883 (and named *Camelus bactrianus ferus*), is believed to survive in the wild in southwest Mongolia, Kansu, Tsinghai, and Sinkiang (HEPTNER et al. 1966; GRUBB 1993). Recent investigations have shown that the hypothesis of an early third millennium BC centre of domestication of the two-humped camel in eastern Iran or in southern Turkmenistan (COMPAGNONI and TOSI 1978) cannot be maintained any longer, since there is no proof whatsoever, that the Holocene distribution area of the two-humped wild camel included this region (PETERS and VON DEN DRIESCH 1997).

Certain authors consider the two-humped wild camel to be the common ancestor of the two domestic forms, Arabian and Bactrian camels being breeds of the same species (e.g. HERRE and RÖHRS 1973), though they may have originated from two different subspecies (KÖHLER 1981; HERRE and RÖHRS 1990). The common ancestry is based on the observation that (1) fertile offspring can be produced from mating one-humped and two-humped camels, (2) the embryos of the two forms have two hump primordia, which fuse in the dromedary during subsequent foetal development (LOMBARDINI 1879) and (3) the fact that there was no evidence for the presence of a one-humped wild camel during Middle Pleistocene to Holocene times in the Afrolevantine region, for *Camelus thomasi* Pomel, 1893, a large camel species inhabiting North Africa and the southwestern Levant, was considered osteologically to belong to the lineage of Asiatic camels (GAUTIER 1966).

Arguments contradicting the hypothesis of the Arabian and the Bactrian camel representing one species include the differences in outer appearance, ecophysiological adaptations, and zoogeographic range of the two domestic forms and the fact that continued crossbreeding rapidly results in loss of fertility (Kolpakov 1935). It was assumed that domestic one-humped camels must have originated from a wild ancestor present in Arabia at some date prior to the 3rd millennium BC, because dromedary remains from archaeological contexts of younger date, for example from urban sites at the east coast of the Arabian Peninsula, probably represent domesticated animals (Hoch 1979; Uerpmann 1987).

In the past, research on the ancestry of domestic camels has been hampered by the general belief that postcranial elements of one-humped and two-humped animals could not be separated morphologically. Some distinguishing postcranial features have been discussed by Lesbre (1903) and Wapnish (1984), but the osteomorphology of the entire postcranial skeleton of the Arabian and Bactrian camel has only recently been covered in detail and on a statistical basis by Steiger (1990). The results of this study have been used to check the taxonomic status of *Camelus thomasi*, probably the only species of wild camel that occurred during the Middle and Late Pleistocene in North Africa and the Levant. Though it was not possible to obtain the *C. thomasi* type specimens, collected from an Acheulian context at Ternifine (Algeria) and described by Pomel (1893), the Upper Palaeolithic camel bones recovered from site 1040 by members of the Combined Nubian Prehistory and Geological Campaign in northern Sudan, studied by Gautier (1966), could be re-analysed morphologically. As a result, the current opinion of *C. thomasi* being closely related to the two-humped camel must be rejected, because the available fossil material (distal humerus, distal radius-ulna, distal tibia, and calcaneus) exhibits features that are characteristic for the one-humped camel (see Steiger 1990 for details), i. e. the more pronounced crista epicondyli lateralis in the humerus, the larger, more distally located medial epicondyle and the more concave palmar articular surface for the os carpi radiale in the radius, and the different proportions of the articular facets for the lateral malleolus and the more acute medial margin of the tibia; as to the calcaneus, its distinctive features are given in figure 1.

Apparently the afrolevantine and central Asian populations of wild camels became separated genetically, perhaps during Lower Pleistocene times, for remains of *C. thomasi* have been recorded from post-Villafranchian, Middle Pleistocene levels (Arambourg 1962). Morphologically the Pleistocene *C. thomasi* represents a dromedary, and the species can therefore be considered a possible ancestor of the domestic one-humped camel.

Toward the end of the Pleistocene *C. thomasi* became extinct in North Africa, for it is not recorded from Holocene deposits (e. g. Peters 1992), nor is it depicted in Holocene rock art (Muzzolini 1986) from that region. However, a one-humped wild camel likely survived in south-western Asia, as is suggested by rock art (e. g. Anati 1968; Zarins 1989) and bone finds, for example from the pre-pottery neolithic site of Ain el-Assad in the eastern Jordanian desert (Turnbull 1989). The calibrated radiocarbon date of c. 7 200–7 100 yr BC, obtained on a dromedary mandible excavated from a shell midden at Sihi on the Red Sea coast of Saudi Arabia (Grigson et al. 1989), apparently was flawed (Clutton-Brock, pers. comm. 1997). Interestingly, the early Holocene camel bones from Ain el-Assad match well with those of modern Arabian camels, whereas the Pleistocene *C. thomasi* remains came from individuals that surpassed modern domestic animals in size up to 20% or more. Provided that this difference in bone size is not an artefact due to the limited sample size, two explanations can be offered. Perhaps the Holocene finds represent a separate species that developed from *C. thomasi* or a common ancestor at a much earlier stage. However, this is not visible in the Pleistocene faunal record of south-western Asia. In fact, none of the "dromedary-sized" camel remains collected from Pleistocene levels in the Levant, submitted for direct radiocarbon dating, proved to be older

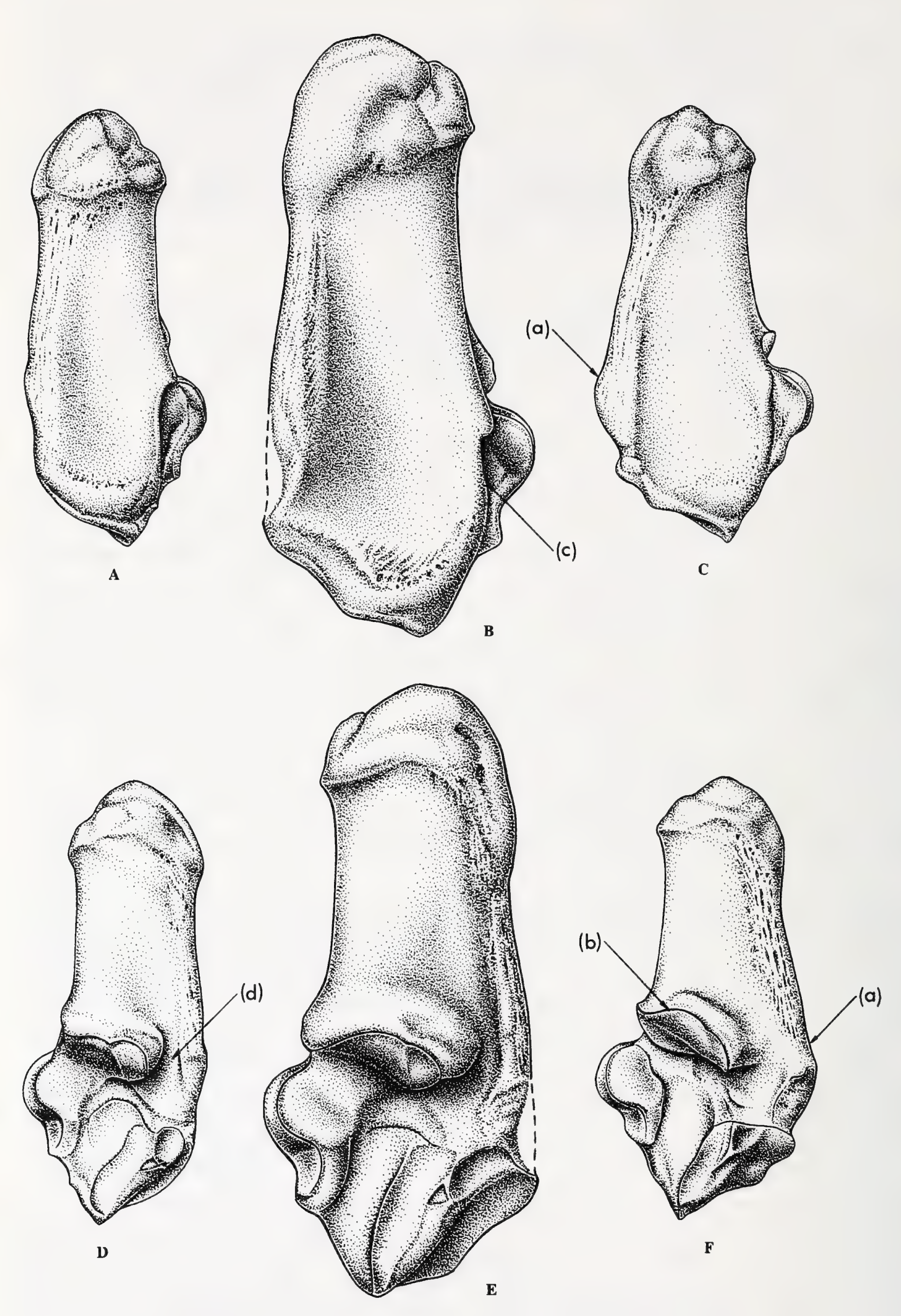


Fig. 1. Calcaneus of Arabian camel (A, D), *Camelus thomasi* (B, E) and Bactrian camel (C, F), lateral and medial view. The distinction between the calcanei of Arabian camel and *C. thomasi* versus Bactrian camel is based on morphological differences in (a) the course of the medioplantar margin, (b) the position of the sustentaculum tali, (c) the lateroplantar margin of the processus coracoideus, and (d) the depth of the sulcus plantar of the sustentaculum tali.

than the 2nd millennium BC (Hedges et al. 1987). An alternative explanation may be that *C. thomasi* underwent a reduction in body size at the transition from the Pleistocene to the Holocene. Such a decrease in body size has been observed in other late Quaternary artiodactyls of the Levant such as wild boar, aurochs, and wild goat (Davis 1987), and it can be assumed that populations of *C. thomasi*, living under similar ecological and/ or climatological constraints, were also affected by this phenomenon.

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Endoscopic observations on tunnel blocking behaviour in the European ground squirrel (*Spermophilus citellus*)

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Key words: *Spermophilus citellus*, tunnel block, burrow, respiration physiology, predation

The use of endoscopic equipment in field studies enables researchers to observe the behaviour of ground-dwelling animals inside their burrows. The burrows of the European ground squirrel (*Spermophilus citellus*) are suitable for studying subterranean behaviour by use of this method, both because of the tunnel size (approximately 5–10 cm in diameter) and their visibility in the field. Each adult ground squirrel occupies one burrow system, which is relatively simple. Typically, the number of entrances varies between one and five, while the length of each tunnel measures between 0.7 and 4.5 m, at a maximal depth of 2 m. The nest chamber can be found at a depth of about 0.5 to 1 m (Ružić 1978).

We investigated burrows of the European ground squirrel in the Kiskunság Nemzeti Park at Bugac Puszta, Hungary (46°38′ N; 19°40′ E). The burrows were inspected from 21. 07. to 08. 08. 1997, using a 205 cm long, manoeuvrable fibre optic industrial endoscope (Olympus), attached to a video system. In total, we investigated 87 entrances of ground squirrel burrows in an area of approximately 3.5 ha.

In 71 cases (82%) a tunnel block was detected at an average distance of 57 cm (sd 30 cm; range: 20–170 cm) from the entrance. In the remaining 16 cases, a) there was either a dead end to the tunnel (9 cases), b) the endoscope got stuck (4 cases), c) the endoscope was too short (1 case), d) or a U-shaped tunnel caused the endoscope to emerge from another entrance (2 cases). In four cases we were able to push the endoscope through the tunnel block. This enabled us to measure the length of these tunnel blocks, which were 30, 30, 40, and 40 cm, respectively (to the nearest 5 cm). There was a clear distinction between dead-ending tunnels and tunnel blocks. A dead-ending tunnel was found to have a smooth cup at the end and always a heap of sand outside the entrance. Blocked tunnels, however, were always filled with loose sand, sometimes with some plant material. 52 of these blocked tunnels (73%) had no sand heap outside, therefore they must have been dug from the inside (Ružić 1978). In three cases a ground squirrel was actually observed while blocking its tunnel. These ground squirrels used mainly the front legs for digging through the sand block, while upward movements with the head were used to close the tunnel block from the inside. The final result was indistinguishable from tunnel blocks observed otherwise. An impression of a tunnel block in a ground squirrel burrow is presented in figure 1.

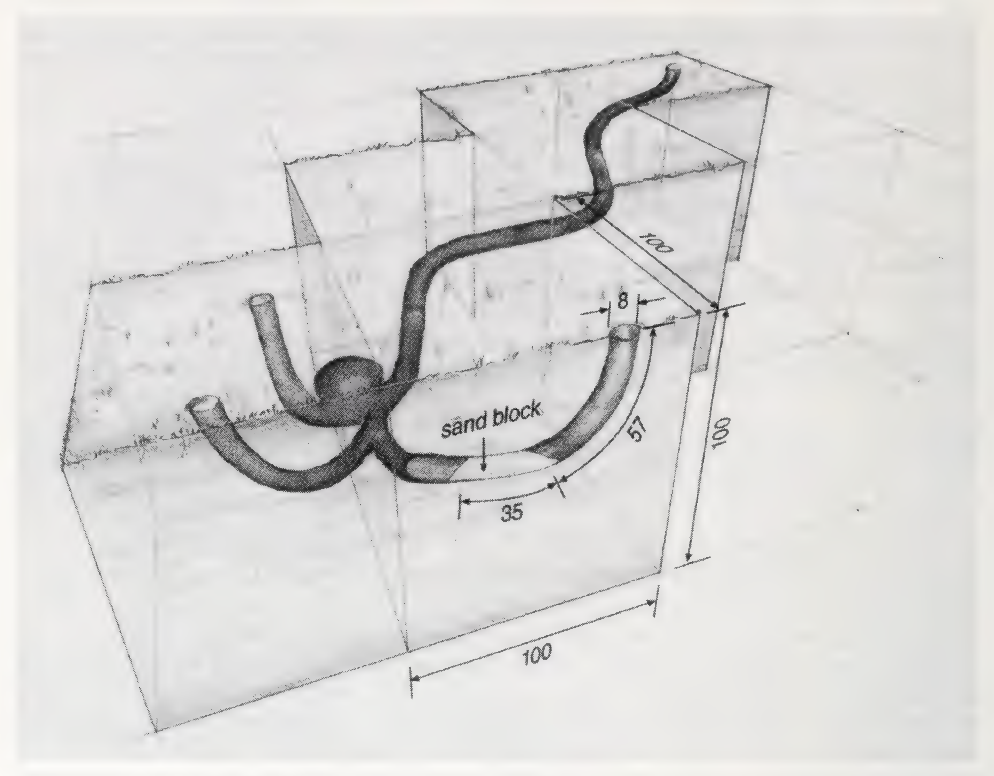


Fig. 1. Impression of a tunnel block in a ground squirrel burrow, excavated near the study area. Measures (in cm) are averages as mentioned in the text. The nest chamber was located at 50 cm below the surface, the deepest point of the burrow at 90 cm below the surface.

It is unlikely that insertion of the endoscope caused the ground squirrels to block their tunnels for two reasons. Firstly, 22 of the burrows were inspected at least 1 hour after the end of the activity phase of the ground squirrels which was measured to be approximately at 18:00 h MET in late July. Of these cases, 21 (95%) were found to be blocked. The one which was not, contained remainders of a tunnel block at 56 cm, and a dead juvenile ground squirrel at 110 cm from the entrance. Secondly, in six other cases we inserted the endoscope in a burrow from which a ground squirrel had just been caught by trapping at the burrow entrance. Here, we also found tunnel blocks at an average distance of 50 cm from the entrance. This suggests that the ground squirrels also block their tunnels while leaving their burrows, even when there is no direct disturbance due to the endoscope or due to people at the site of the burrow. After releasing these animals in their burrows, their behaviour was observed with the endoscope already placed in the tunnel. In all cases the ground squirrels dug their way through the tunnel block within a few seconds, closing it behind them as described above.

We suggest that free-ranging European ground squirrels are actively avoiding predation by blocking their burrow tunnels with sand, a behaviour that was also found in wood mice in the laboratory (KHIDAS and HANSELL 1995). They do so both when entering and leaving their burrows. We suppose that ground squirrel predators in the area, such as the large whip snake (*Coluber jugularis*), the weasel (*Mustela nivalis*), the common polecat (*Mustela putorius*), and the step polecat (*Mustela eversmanni*) will be less successful in hunting ground squirrels from their burrows when the tunnels are blocked. Furthermore,

blocking a tunnel at 57 cm distance from the entrance may have the advantage that the block distant from the entrance still leaves the ground squirrel with a quick refuge against (aerial-) predators while being at the surface.

An important consequence of this behaviour might be that the ground squirrels exclude themselves largely from any outside information, such as time of day or weather conditions while being inside a blocked burrow. Another consequence is the loss of mass air flow, which should have an important effect on the concentration of respiratory gases (Wilson and Kilgore 1978; Withers 1978). Low O_2 and high CO_2 concentrations have indeed been measured in ground squirrel burrows during the active season (McArthur and Milsom 1991 a; Maclean 1981; Baudinette 1974). From this, one would also expect ground squirrels to have a high tolerance to hypoxia and hypercapnia, which was shown in the Columbian and golden-mantled ground squirrel (McArthur and Milsom 1991 b). To our knowledge, however, tunnel blocking behaviour has not previously been described in ground squirrels.

It is important to distinguish between hibernation-associated entrance blocking (Ružić 1978), and tunnel blocking during the active season. Firstly, the period in which this study was performed was before the onset of the hibernation season in the European ground squirrel. This is illustrated by the fact that during the study period we caught several adult females, which are the first to start hibernation in the European ground squirrel (Millesi et al. 1998). Secondly, hibernation-associated blocking occurs at the entrance, and not at an average distance of 57 cm from the entrance, where we found the tunnel blocks during the active season.

To our knowledge, this is the first field study describing tunnel blocking behaviour in a ground-dwelling mammal. The description of this behaviour may have important implications for interpreting studies on activity patterns, respiration physiology, and predation in ground-dwelling mammals.

Acknowledgements

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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MITTEILUNGEN DER GESELLSCHAFT

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 21. September 1998 im Hörsaal des Karolinums, Prag.

Der 1. Vorsitzende, Herr ERKERT, eröffnet die Versammlung um 16.30 Uhr.

1. Die Tagesordnung wird angenommen.
2. Herr SCHRÖPFER verliest den Bericht über das Jahr 1997. Auf Einladung der Kollegen MARTIN FISCHER (Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum) und STEFAN HALLE (Institut für Ökologie) fand die 71. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde vom 21.–25. September 1997 in Jena statt. In 41 Vorträgen und 20 Poster-Präsentationen zu den Schwerpunktthemen „Motorik bei Säugetieren“, „Methoden säugetierkundlicher Freilandforschung“, „Biologie der Musteliden“ sowie zu freien Themen bekamen 170 Teilnehmer ein vielseitiges wissenschaftliches Programm geboten. Eine Exkursion zur BREHM-Gedenkstätte nach Renthendorf und eine Wanderung um Jena erwiesen sich als biologisch wie geschichtlich gleichermaßen eindrückliches Ergänzungsprogramm. Dafür, daß unsere Gesellschaft zum ersten Mal nach der Wiedervereinigung in einem der neuen Bundesländer tagen konnte, spricht Herr SCHRÖPFER den Veranstaltern, ihren Mitarbeiterinnen und Mitarbeitern seinen herzlichen Dank aus.

   Die Preise des Poster-Wettbewerbs der Jenaer Tagung gingen an

   1. K. KUGELSCHAFTER, B. LUDWIG, S. ECK und A. WECKERT: „Testverfahren zur Prüfung der Wirksamkeit von „Automarder“-Abwehrmitteln *Martes foina* (Erxleben, 1777)“.
   2. K. ECKHOFF und H. KLINGEL: „Radiotelemetrie an der ungestreiften Grasratte (*Arvicanthis niloticus*)“.
   3. B. LUDWIG: „Sozialverhalten und Kommunikation von Baummardern (*Martes martes* L., 1758) unter Gehegebedingungen“.

   Band 62 der Zeitschrift für Säugetierkunde erschien in sechs Heften mit insgesamt 384 Seiten. Er enthielt 32 wissenschaftliche Originalarbeiten, 15 Kurzmitteilungen, neun Buchbesprechungen und zwei Mitteilungen der Gesellschaft. Den beiden Schriftleitern und den Mitarbeitern des wissenschaftlichen Beirates wird ebenso gedankt wie dem Gustav Fischer Verlag Jena.
   Weiterhin gab die Gesellschaft wie in den Vorjahren ein Supplementheft heraus, das die 71. Jahrestagung der Gesellschaft in Jena zum Inhalt hat. Ferner erschien ein Supplementum II als „Proceedings of the 1st International Symposium of Physiology and Ethology of Wild and Zoo Animals“.

   Die Mitgliederzahl betrug Ende 1997 603.

   Durch Tod verlor die Gesellschaft folgende Mitglieder:
   FRANZ BOECKER (Mitglied seit 1961),
   Drs. h. c. FRIEDRICH GEORGI (Mitglied seit 1971),
   Prof. Dr. Dr. h. c. WOLF HERRE (Ehrenmitglied, Mitglied seit 1954),
   Prof. Dr. PAUL LEYHAUSEN (Mitglied seit 1954),
   Prof. Dr. JOCHEN NIETHAMMER (Mitglied seit 1958).

3. Herr Schröpfer erläutert den von Frau Kühnrich vorgelegten Kassenbericht und dankt der Schatzmeisterin für ihre sorgfältige und umfangreiche Arbeit.

4. Die Herren Bohlken und Schliemann haben die Kontounterlagen der Gesellschaft in Hamburg geprüft und für korrekt befunden.

5. Die Anträge auf Entlastung der Schatzmeisterin und des Vorstandes werden bei fünf Enthaltungen angenommen.

6. Die Herren Bohlken und Schliemann werden als Kassenprüfer für das Jahr 1998 wiedergewählt. Beide sind mit der Wahl einverstanden.

7. Der Vorstand schlägt vor, die Mitgliedsbeiträge für 1999 unverändert zu lassen. Die Anwesenden sind damit einverstanden.

8. Die Mitgliederversammlung nimmt die Einladung von Herrn Flösser an, die 73. Jahrestagung vom 26.–30. September 1999 in Bad Dürkheim abzuhalten. Als Schwerpunktthemen sind vorgesehen Wildbiologie, Sinnesphysiologie, Ökologie und Verhalten der Rodentia. Das Programm wird ergänzt durch eine Exkursion in den Nationalpark Pfälzer Wald.

   Der Vorstand beabsichtigt, die Jahrestagung 2000 entweder in Essen abzuhalten oder – in Zusammenarbeit mit der Vereniging voor Zoogdierkunde en Zoogdierbescherming (VZZ) – an einem Ort in den Niederlanden. Beide Möglichkeiten werden derzeit geprüft. Als Tagungsort für 2001 ist Berlin vorgesehen (75 Jahre DGS).

9. Frau Feddersen-Petersen, von der ein Positionspapier zum Thema Tierversuche vorliegt, bittet den Vorstand, sie von ihrer Position als Vorsitzende der Tierschutzkommission zu entbinden. Es wird empfohlen, Herrn Rehkämper zu bitten, die Arbeit kommissarisch weiterzuführen, bis eine neue Kommission benannt werden kann.

   In Jena hat Herr Pelz die Nachfolge von Herrn Schröpfer als Vorsitzender der Artenschutzkommission angetreten. Die Arbeitsgruppe „Bisam“ besteht nicht mehr.

Die Sitzung endet um 17.45 Uhr

Prof. Dr. H. Erkert	Prof. Dr. R. Schröpfer	Dr. H. Frädrich
1. Vorsitzender	Geschäftsführer	Schriftführer

4th International Symposium Isolated Vertebrate Communication in the Tropics May 13–17, 1999 in Bonn, Germany

The 4th international symposium on evolution and ecology of tropical animals will be held by the Zoologisches Forschungsinstitut und Museum Alexander König (Bonn/Germany) May 13–17, 1999. Main topic of the symposium will be evolutionary processes in vertebrate communities of isolated habitats in the tropics. Theoretical and applied contributions are welcome. Studies on non-vertebrates, contributing to our knowledge in vertebrates will be considered, too.

The symposium and the lodging-place of the participants will be at the Gustav-Stresemann-Institute, a conference centre, situated close to our institute.

For further information and announcements please contact: Prof. Dr. W. Böhme, Adenauerallee 160, 53113 Bonn, Germany (tel.: +49 228 91 22 250, fax: ++49 228 216 979, e-mail: r.hutterer.zfmk@uni-bonn.de)

4th International Conference on Dormice (Gliridae, Rodentia). September 13–16, 1999 in Edirne, Turkey

This meeting will take place in Trakya University, Edirne, Turkey from 13th to 16th of September. All aspects of dormice biology are considered. Further information is available on the web page: http://www.trakya.edu.tr

Interested mammalogists may contact: Prof. Dr. Cengiz Kurtonur, Trakya University, 22030 Edirne, Turkey, Fax: +90 284 212 09 61; e-mail: cengizk@aix.trakya.edu.tr

2nd European Beaver Symposium 2000 – Preliminary information –

The 2nd European Beaver Symposium will be held in the Bialowieza Primeval Forest in September 2000. It will be hosted by the Castor Research Society – a non-governmental organisation promoting research relating to the European beaver – in cooperation with the Institute of Environmental Biology at Jagiellonian University.

The 2nd European Beaver Symposium will offer a full programme of lecture presentations, poster sessions, workshops and field trips, including an excursion to the Popielno Research Station. All aspects of beaver biology will be considered.

For further information please contact: Andrzej Czech, Department of Hydrobiology; Institute of Environmental Biology, Jagiellonian University, Oleandry 2a, 30-063 Krakow, Poland; Tel.: ++48 12 633 77 ext. 480; Fax. ++48 12 634 19 78; e-mail: czech@eko.eko.uj.edu.pl or: czech@jetta.if.uj.edu.pl

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Buchbesprechung

Stevens, C. E.; Hume, I. D.: **Comparative physiology of the vertebrate digestive system.** Second Ed. Cambridge, New York, Melbourne: Cambridge University Press 1995. Hardback, 400 pp. US$ 80.00. ISBN 0-521-44418-7.

The second edition of this book, now jointly authored by C. E. Stevens from the College of Veterinary Medicine of North Carolina State University and I. D. Hume of the School of Biological Sciences of the University of Sydney, is a much expanded (from 300 to 400 pages) version of the first edition, which was published in 1988 by Stevens alone. New chapters on "Energy and nutritional requirements", on "Digesta transit and retention" and on the "Evolution of the digestive system" were included and many new research results added. The wealth of data published in the volume is very impressive. Such a book will find favour among readers from very different fields of science. Not only those interested in physiology will appreciate this remarkable publication, but also veterinarians, nutritionists, anatomists, and zoologists in general, to name just a few.

The characteristic illustrations published by Stevens in the first edition can also be found in the present volume. Some colleagues called them "radiator pictures" because of the schematic zig-zag position of the small and large intestines in these drawings. This comment was not always meant positively, but these semischematic presentations make differences in the general composition of the gastrointestinal tract clearly visible and stimulate comparisons. The complex topography of the digestive tract in the abdomen is, most probably, much more influenced by the availability of intraperitoneal volume than by aspects of comparative nutritional physiology.

The present reviewer found the new chapter on aspects of evolution of the digestive system especially interesting. In it Stevens and Hume also consider invertebrates, but in most cases this does not really help to improve the understanding in vertebrates. Today, a discussion of "evolution" of the digestive process and the digestive tract in vertebrates still presents considerable problems. Only few data that help to understand the process of evolutionary differentiation in digestive physiology can be presented! Two examples may illustrate this point: In the case of birds (page 309) and mammals (pages 310 and 311) the authors speak of "major types of digestive strategies practiced" by these vertebrates, but the respective illustrations depict different types of morphological differentiations of digestive tracts. Presently, it is still necessary in many cases to extrapolate function from morphology! Another example is the short section on cetaceans (whales) on page 317. The recent findings indicating "a close relationship between the cetaceans and artiodactyls" "could account for the complex cetacean forestomach". This might well be so, but it should be mentioned in this book that the morphology of the digestive tract in whales and even-hoved mammals is remarkably different – and the digestive process, very probably, differs as well!

The above haphazardly picked examples of criticism do not at all diminish the positive impression given by this fine book. The authors can only be admired for the gigantic amount of data they discuss; their list of references comprises 62 pages! An index of 10 pages makes the contents of the text accessible. The inaccurate spelling of many non-English words in the list of references is a general problem in many books published in English. The editorial office of the publisher should have checked and corrected the misspellings that can, e.g., be found in the titles of the publications by Ruckebusch et al. (1970), Harder (1950), and Pernkopf (1930, 1937).

P. Langer, Giessen

Instructions to Authors

Submission and Acceptance of Manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel, Germany, e-mail: dkruska@ifh.uni-kiel.de. Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by mail, and as soon as the peer reviews are received the authors will be informed concerning the decision for acceptance.

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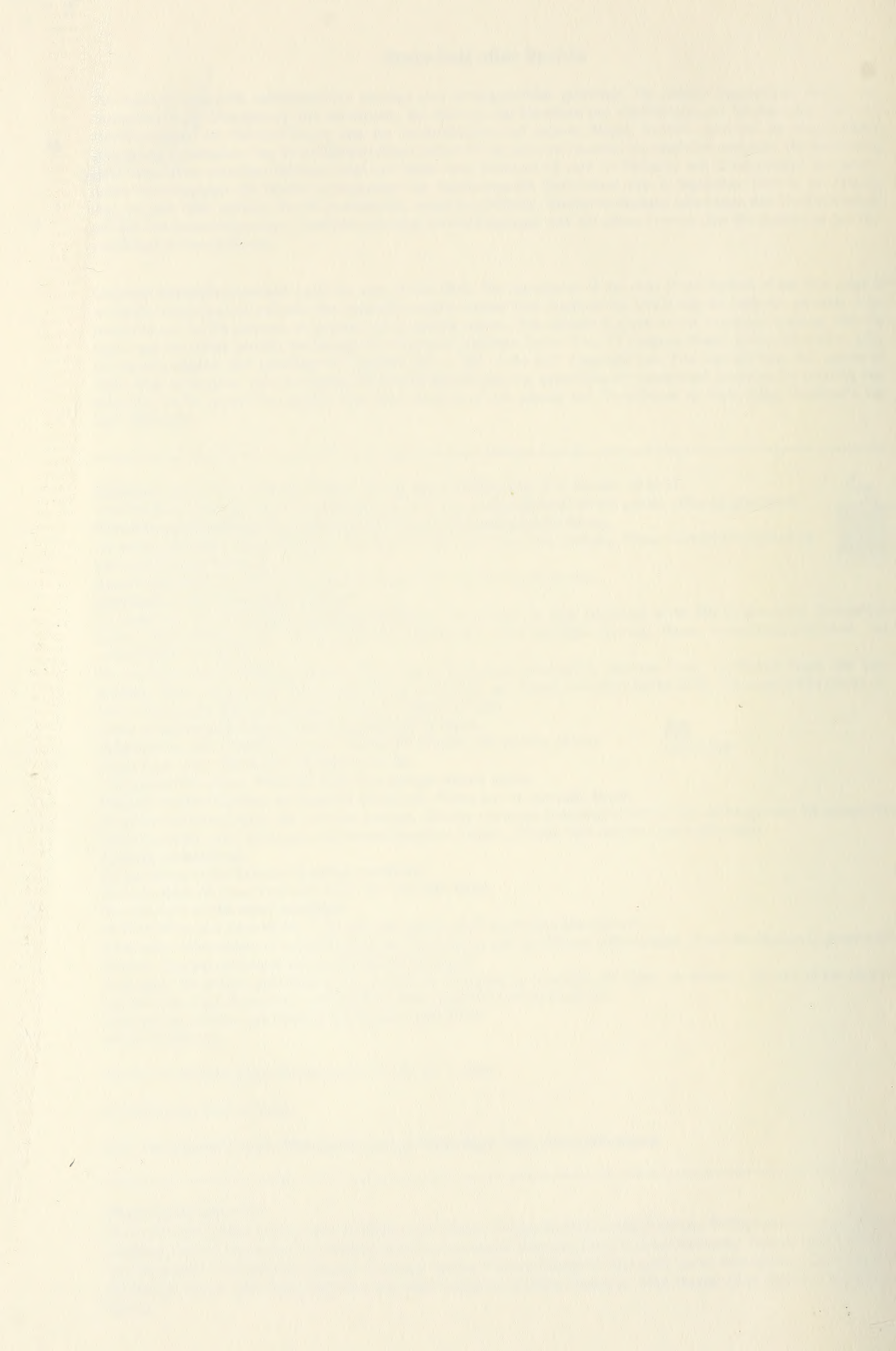
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